ANNALS
OF THE
ENTOMOLOGICAL SOCIETY
OF AMERICA

Volume 52 November, 1959 Number 6

ANNALS OF THE ENTOMOLOGICAL SOCIETY OF AMERICA

Published by the

ENTOMOLOGICAL SOCIETY OF AMERICA

R. H. NELSON, *Executive Secretary*
1530 P Street, N. W.
Washington 5, D. C.

ROLAND F. HUSSEY, *Editor*
Department of Biology
University of Florida,
Gainesville, Florida

F. W. POOS, *Managing Editor*
1530 P Street, N. W.,
Washington 5, D. C.

EDITORIAL BOARD

M. H. HATCH, *Chairman*, Seattle, Wash. (A, 1959)
L. E. ROZEBOOM, Baltimore, Md. (D, 1960)
J. A. ADAMS, Poughkeepsie, N. Y. (C, 1961)
J. J. PRATT, Wayland, Mass. (B, 1962)
F. N. YOUNG, Bloomington, Ind. (A, 1963)

A bimonthly journal published on the 15th of January, March, May, July, September, November, devoted to the interest of classical entomology. Authors are entirely responsible for statements in the *Annals*, whether of fact or opinion.

TERMS OF SUBSCRIPTION. Non-members in North America and U. S. Possessions—$15.00 per year; elsewhere—$15.00 plus 60¢ postage. Single copies $3.00. **Deliveries overseas** are not guaranteed and foreign mailings are made at the subscriber's risk.

A *single order* for the Annals of the Entomological Society of America and the Journal of Economic Entomology, *if sent to the same address*, may be obtained at a **COMBINATION PRICE** of $27.00 per year, domestic; $28.20 foreign.

LOST NUMBERS. Missing numbers cannot be supplied free of charge unless notice is received within 60 days after the appearance of issues concerned.

BACK NUMBERS. The Executive Secretary will be glad to quote prices upon request.

REPRINTS. No gratis copies are supplied. A schedule of prices which will apply to orders received before the Annals is printed, and an order form are sent with proof. For price schedule, see Bulletin of the Entomological Society of America, Vol. 1, No. 4, December, 1955, or page 509 of Vol. 49(5) of the *Annals*.

BUSINESS COMMUNICATIONS of the Society and **SUBSCRIPTIONS AND MATTERS PERTAINING TO ADVERTISEMENTS** should be sent to the Executive Secretary, Entomological Society of America, 1530 P Street, N. W., Washington 5, D. C. Changes of address must reach the office of the Executive Secretary 5 days prior to the month of issue to be effective for that month. Members should make use of the postal regulations which provide for forwarding of second class mail if postage upon delivery is guaranteed.

ALL MANUSCRIPTS and other copy for the *Annals* should be sent to the Executive Secretary. Prompt publication of acceptable matter may be secured by payment of the cost of printing and engraving ($18.00 per page plus cost of engravings with additional charge for excessive tabular matter). Cost of engravings in excess of $20.00 for each eight printed pages or major fraction thereof, will be charged to the author. Before preparing manuscripts for publication in the *Annals*, authors are urged to consult the Publication Policies and Manuscript Rules and Suggestions given in Vol 49(5): 506–9, September 1956.

Second class postage paid at Columbus, Ohio. By order of Dec. 10, 1958.

Printed by The Spahr & Glenn Company,
50 East Broad Street
Columbus 15, Ohio, U. S. A.

Issued November 30, 1959

Annals of
The Entomological Society of America

Volume 52 NOVEMBER, 1959 No. 6

OXYGEN POISONING IN INSECTS[1]

ARNOLD M. CLARK
Biology Department, University of Delaware, Newark, Delaware

ABSTRACT

Pupae of *Bracon hebetor*, *Grapholitha molesta*, *Anagasta kühniella*, *Galleria mellonella*, *Prodenia eridania*, *Tenebrio molitor*, and *Epilachna varivestis* showed arrestment of development and decreased oxygen consumption after exposure to oxygen at 75 pounds pressure; with *P. eridania* and *G. mellonella* such exposure for 5 minutes produced paralysis which was not reversible. Pupae of *Drosophila melanogaster*, *Phormia regina*, and *Apis mellifera* were not affected by exposure to oxygen, nor were larvae of *B. hebetor*, *T. molitor*, *A. kühniella*, or *P. regina*. Pupae of *T. molitor* that matured as adults after exposure to oxygen at 30 pounds pressure apparently had difficulty in removing their pupal exuviae and their wings were abnormal.

High pressures of oxygen have been shown to have deleterious effects on a wide range of organisms (Bert 1878; Stadie et al. 1944; Bean 1945). Although as early as 1878 oxygen had been shown to injure insects, there is little literature on the subject. A few papers have appeared, however, and these indicate that a variety of effects caused by oxygen can be investigated in more detail. An effect from oxygen upon the neuromuscular apparatus of *Drosophila azteca* adults has been shown by Williams and Beecher (1944), and upon the pupae of *Mormoniella vitripennis* by Goldsmith and Schneiderman (1956). An effect of oxygen upon development has been reported by Glass and Plaine (1952) for *Drosophila melanogaster* exposed as embryos, by Clark and Herr (1954) for *Habrobracon juglandis* (=*Bracon hebetor*) pupae, and by Goldsmith and Schneiderman (1956) for *Mormoniella* of various postembryonic stages; an arrestment of pigmentation and a decrease in oxygen consumption was reported for *Habrobracon* (=*Bracon*) pupae exposed to oxygen (Clark and Herr 1954). These reports on a few insects indicate that oxygen poisoning may be of general occurrence among insects. In the present paper some effects of oxygen upon 11 species of insects are reported.

MATERIALS AND METHODS

The insects used in this study are listed below.[2] All of these were exposed to oxygen during the pupal stage of development. For some of the species, however, the larval stages were also treated. Two criteria of oxygen effects were used (1) the ability of the organisms to continue their development and to emerge as adults and, (2) the modification in the rate at which they consume oxygen. The insects to be treated were placed into a cylindrical chamber (600 cm³). The air in the chamber was replaced by oxygen. The oxygen was then applied under pressure (from 15 to 75 pounds) for 1 minute to 10 minutes. The precise dosage for each species of insect is given in tables 1 and 2. Nitrogen and air were also used and compared with the oxygen. After

[1]Research carried out under AEC contract AT(30-1)-1752 between the University of Delaware and the U. S. Atomic Energy Commission. Accepted for publication December 28, 1958.

[2]*Anagasta kühniella* (Zell.), Mediterranean flour moth.
Apis mellifera L., honey bee. Obtained as larvae from Dr. A. S. Michaels, U.S.D.A., Beltsville, Md.
Bracon hebetor Say (=*Habrobracon juglandis* Ashm.).
Drosophila melanogaster Meig., fruit fly.
Epilachna varivestis Muls., Mexican bean beetle. Obtained as pupae from Dr. Keith Ihde, Hercules Powder Company, Wilmington, Del.
Galleria mellonella (L.), greater wax moth. Obtained as larvae from U.S.D.A., Beltsville, Md.
Grapholitha molesta (Busck), oriental fruit moth. Obtained as larvae from Mr. M. Brunson, U.S.D.A., Moorestown, N. J.
Musca domestica L., house fly. Obtained as larvae from Hercules Powder Company.
Phormia regina (Meig.), black blow fly. Obtained as larvae from Dr. Charles Hassett, Army Chemical Center, Maryland.
Prodenia eridania (Cram.) southern armyworm. Obtained as larvae or pupae from Hercules Powder Company.
Tenebrio molitor L., yellow mealworm. Obtained as larvae from Carolina Biological Supply Company, Elon College, N. C.

I wish to thank the members of these institutions for their helpfulness. The experimental work reported here was carried out with the assistance of Miss Mary Ann Rubin.

treatment, the insects were placed into an incubator (30° C.) and observed for development to the adult stage or were placed immediately into the Warburg apparatus in order to measure the rate of oxygen consumption. For *Prodenia* and *Galleria* a "paralysis effect" was observed and studied.

RESULTS

The development of pupae to the adult stage is prevented by exposure to oxygen for some species but not for others (table 1). For *Grapholitha*, for example, of 80 pupae that were exposed to 75 pounds of oxygen for 5 minutes, four developed to the adult stage, while for the pupae exposed to air (15 pounds of air) 55 out of 70, and for the nitrogen-treated pupae (75 pounds of nitrogen) 67 out of 80 developed to the adult stage. These differences in the proportion of pupae that become adults is shown in the last column of table 1. Exposure to 75 pounds of oxygen prevented a significant proportion of *Grapholitha*, *Prodenia*, *Anagasta*, *Galleria*, *Tenebrio*, and *Epilachna* from becoming adults but had no deleterious effect upon the development of *Musca*, *Drosophila*, *Phormia*, and *Apis* pupae. Detailed studies for *Bracon* have shown that even 15 pounds of oxygen will prevent the development of about 50 percent of the treated pupae (Clark and Papa 1958). Injurious effects on development from doses of oxygen below 75 pounds have been shown for some of the insects in this study, but sufficient data are not yet available for comparison of the relative sensitivities of these insects.

The pupae of *Tenebrio* and *Galleria* are injured more by 75 pounds of air than by 15 pounds of 100 percent oxygen (table 1). It appears to be true also for *Bracon* and for *Anagasta* pupae that air delivered at higher pressures is more injurious than is 100 percent oxygen of the same oxygen tension. The reason for this is not clear at present.

A decrease in the rate of oxygen consumption occurs for oxygen-treated pupae of *Grapholitha*,

Table 1.—Incidence of pupae developing to the adult stage after exposure to oxygen gas.

Name of insect	Gas	Pressure (pounds)	Duration (minutes)	No. treated	No. of adults	Incidence of adults
Grapholitha molesta	Air	15	—	70	55	0.79
	O_2	75	5	80	4	.05
	N_2	75	5	80	67	.84
Prodenia eridania	Air	15	—	11	11	1.00
	O_2	75	5	11	1	.09
	N_2	75	5	11	11	1.00
Anagasta kühniella	Air	15	—	30	28	.93
	O_2	75	5	30	1	.03
	N_2	75	5	30	30	1.00
	Air	75	5	14	3	.21
	O_2	30	5	29	7	.24
Galleria mellonella	Air	15	—	40	39	.98
	O_2	75	5	30	6	.20
	N_2	75	5	30	27	.90
	Air	75	5	10	4	.40
	O_2	30	5	10	10	1.00
	N_2	30	5	10	10	1.00
Tenebrio molitor	Air	15	—	15	15	1.00
	O_2	75	5	30	0	0
	N_2	75	5	10	10	1.00
	Air	75	5	15	2	.13
	O_2	15	5	15	15	1.00
Epilachna varivestis	Air	15	—	23	23	1.00
	O_2	75	5	27	13	.48
	N_2	75	5	24	24	1.00
Musca domestica	Air	15	—	75	72	.96
	O_2	75	10	75	70	.93
Drosophila melanogaster	Air	15	—	100	68	.68
	O_2	75	10	100	79	.79
Phormia regina	Air	15	—	25	25	1.00
	O_2	75	5	25	25	1.00
	N_2	75	5	25	24	.96
Bracon hebetor	Air	15	—	300	242	0.81
	O_2	15	1	200	106	.53
	Air	30	1	200	163	.81
	Air	45	1	200	23	.11
Apis mellifera	Air	15	—	15	15	1.00
	O_2	75	5	15	15	1.00
	N_2	75	5	15	15	1.00

Prodenia, *Anagasta*, *Galleria*, *Tenebrio*, and *Bracon*. *Epilachna* was not tested. No decrease in oxygen consumption was found for *Musca*, *Drosophila*, *Phormia*, and *Apis*. The oxygen consumption is expressed as ml/hr/vessel for all insects except for *Galleria* where the rate of oxygen consumption is expressed as ml/gm/hr. In the last column of table 2 comparison with air controls is presented. For *Grapholitha*, for example, pupae exposed to oxygen consumed 48 percent as much oxygen as the air controls. The oxygen consumption of oxygen-treated pupae of *Bracon*, *Prodenia*, *Anagasta*, *Grapholitha*, and *Galleria* was measured not only within 1 hour after treatment but also after 24 hours. No recovery of oxygen uptake was observed after the 24-hour interval.

Pupae of *Prodenia* and *Galleria* were paralyzed after exposure to 75 pounds of oxygen. Ordinarily, when these pupae are touched they wiggle their abdomens. Paralyzed pupae are unable to wiggle their abdomens. The abdomen becomes rigid. In most cases the pupae were not in a state of paralysis when examined immediately after exposure for 5 minutes to 75 pounds of oxygen. These pupae become paralyzed, however, within 15 minutes. These pupae remain as pupae and in the paralyzed state. There is no recovery.

Pupae of *Tenebrio* that are exposed to 30 pounds of oxygen for 5 minutes continue their development to the adult stage. The wings of some, however, are abnormal and not properly distended. Observation of the young adult shows that it has difficulty in the removal of the exuvia, which may be "sticky" and therefore difficult to remove without injuring the delicate wings.

The larvae of *Bracon*, *Tenebrio*, and *Anagasta* were exposed to doses of oxygen that were sufficiently large to cause injury to the pupae. No arrestment of development was seen and there was no decrease in oxygen consumption. The pupae therefore appear to be more sensitive than the larvae for these species. *Phormia* larvae showed no injury from oxygen when judged by these criteria.

DISCUSSION

The purpose of this present report is to show that oxygen poisoning may be of wide occurrence among insects and that some insects may be extremely sensitive. The ease of handling and the wide variety of effects that they show indicate that insects may be excellent material for the study of oxygen poisoning. Some of the effects are similar to those found for vertebrates and plants.

Table 2.—Oxygen consumption of pupae after exposure to oxygen gas.

Name of insect	Gas	Pressure (pounds)	Duration (minutes)	No. of experiments	No. of pupae per vessel	Oxygen consumed	
						ml/hr/vessel	% of air controls
Grapholitha molesta	Air	15	—	8	10	46	—
	O_2	75	5	9	10	22	48
	N_2	75	5	9	10	50	110
Prodenia eridania	Air	15	—	5	1	46	—
	O_2	75	5	5	1	2	4
	N_2	75	5	4	1	47	102
Anagasta kühniella	Air	15	—	3	5	27	—
	O_2	75	5	3	5	10	37
	N_2	75	5	3	5	30	111
	O_2	30	5	3	5	20	74
Galleria mellonella	Air	15	—	4	1	618*	—
	O_2	75	5	4	1	176*	28
	N_2	75	5	4	1	606*	98
Tenebrio molitor	Air	15	—	10	1	35	—
	O_2	75	5	10	1	22	63
Musca domestica	Air	15	—	5	5	39	—
	O_2	75	10	5	5	39	100
Drosophila melanogaster	Air	15	—	2	50	13	—
	O_2	75	10	2	50	14	110
Phormia regina	Air	15	—	5	5	166	—
	O_2	75	10	5	5	162	98
Bracon hebetor	Air	15	—	11	25	35	—
	O_2	30	1	6	25	5	14
Apis mellifera	Air	15	—	3	1	21	—
	O_2	75	5	3	1	25	119
	N_2	75	5	3	1	20	95

*The oxygen uptake has been calculated as ml/gm/hr for *Galleria*.

There is an arrestment of development. Oxygen-treated pupae remain as pupae. They are not dead, since their oxygen consumption continues, although at a somewhat lowered rate after some treatments. Goldsmith and Schneiderman (1956) have reported similar data for *Mormoniella* pupae. In *Bracon* the arrested pupae are still alive after the controls have become adults. An arrested development has been reported for frog embryos (Malamed 1958) and for wheat roots by Elliasson (1958).

A marked decrease in oxygen consumption can be observed but this requires exposure to oxygen at higher pressures than is necessary to only arrest development (Clark and Papa 1958). The effect of oxygen on oxygen consumption is immediate and there is no recovery. Further, in *Bracon*, protection against damage by oxygen can be obtained by placing pupae at 10° C. for 15 minutes immediately before exposure to oxygen (Clark and Papa 1958). These observations indicate that some metabolic pathway may be blocked. We have found no decrease in succinic dehydrogenase, DPN–malic dehydrogenase, cytochrome oxidase, catalase, or tyrosinase for homogenates even though the whole embryo shows a decrease in oxygen consumption.

Prodenia and *Galleria* pupae seem to be favorable for the study of paralysis since it occurs within 15 minutes after exposure to 75 pounds of oxygen and is irreversible. We are attempting to reverse this paralysis effect and to prevent its occurrence by use of various pre- and post-treatments such as modification of temperature and by injection of substances such as glutathione and ATP. An effect of oxygen upon the neuromuscular system has been reported for adult insects (Williams and Beecher 1944; Goldsmith and Schneiderman 1956). Pupae seem to be more sensitive than adults as judged by this paralysis effect. The neuromuscular effects from oxygen have been observed and stressed in many studies on vertebrates (Bean 1945).

The studies reported here have been carried out primarily on the pupae. Work on *Bracon* has shown that the pupal stage is more sensitive than the larval or the prepupal stages (Clark et al. 1958). There are reports for *Mormoniella* and for *Drosophila* that other stages of development may be more sensitive than the pupal stage. Our work on mature larvae of *Tenebrio*, *Anagasta* and *Phormia* has shown no obvious injury from oxygen but perhaps higher pressures of oxygen will have an affect on development and metabolism. Our work to date seems to indicate that the pupal stage of development may be the stage that is most sensitive to oxygen. Other investigators, however, working on other insects have not reported data to support this generalization.

The four species of Lepidoptera and the two species of Coleoptera reported are oxygen-sensitive while the three species of Diptera are not. Of the Hymenoptera, *Bracon hebetor* is oxygen-sensitive while *Apis mellifera* is oxygen-resistant. Thus, there is at present no obvious pattern of sensitivity that has phylogenetic significance.

REFERENCES CITED

Bean, J. W. 1945. Effects of oxygen at increased pressure. Physiol. Rev. 25: 1–147.

Bert, P. 1878. La pression barometrique. Paris: G. Masson.

Clark, A. M., G. A. Harwitz, and **M. A. Rubin**. 1958. Sensitivity to oxygen during postembryonic development of the wasp *Habrobracon*. Science **127**: 1289-90.

Clark, A. M., and **E. B. Herr, Jr.** 1954. The sensitivity of developing *Habrobracon* to oxygen. Biol. Bull. 107: 329–34.

Clark, A. M., and **M. J. Papa**. 1958. Some effects of oxygen upon the white pupae of *Habrobracon*. Biol. Bull. 114: 180–7.

Eliasson, L. 1958. The inhibitory effect of oxygen on the growth of wheat roots. Physiol. Plantarum 11: 572–84.

Glass, B., and **H. L. Plaine.** 1952. The role of oxygen concentration in determining the effectiveness of X-rays on the action of a specific gene in *Drosophila melanogaster*. Proc. Natl. Acad. Sci. 38: 697–705.

Goldsmith, M. H., and **H. A. Schneiderman.** 1956. Oxygen poisoning in an insect. Anat. Rec. 125: 560.

Malamed, S. 1958. Gastrula blockage in frogs' eggs produced by oxygen poisoning. Biol. Bull. 114: 226–45.

Stadie, W. C., B. C. Riggs, and **N. Haugaard.** 1944. Oxygen poisoning. Amer. Jour. Med. Sci. 207: 84–114.

Williams, C. M., and **H. K. Beecher.** 1944. Sensitivity of *Drosophila* to poisoning by oxygen. Amer. Jour. Physiol. 140: 566–73.

FLIGHT RANGE, DISPERSAL PATTERNS AND POPULATION DENSITY OF THE EYE GNAT, HIPPELATES COLLUSOR[1]

MIR S. MULLA AND RALPH B. MARCH[2]
University of California Citrus Experiment Station, Riverside

ABSTRACT

Gnats tagged with radioactive phosphorus, released in the Palm Desert and Indio areas of the Coachella Valley in southern California, generally dispersed into agricultural areas and adjacent residential sections where favorable conditions existed for their feeding and breeding activities. They avoided virgin desert and barren hills, but were found to cross ½ mile of desert to suitable habitats on the far side. Dispersal occurred both up-wind and down-wind, but the greatest distance travelled in both experiments (4.1 and 4.3 miles, respectively) was with the wind. In one experiment, the population density was estimated at 3 to 5 thousand gnats per acre. Gnats were found resting at night on dry or damp ground, on soil clods, on dried rootlets protruding above the ground, and on foliage of low-growing plants.

Hippelates eye gnats are extremely annoying pests of man and domestic animals in the Coachella Valley of southern California. They fly about persistently and alight on the face, mucous membranes, and other exposed parts of man and animals. They constitute a great nuisance in agricultural and residential areas, school yards, golf courses, and the like. In addition to being a nuisance, they have been incriminated in the transmission of pink eye, an infectious eye disease prevalent among preschool and grammer-school children in this valley (Herms 1926, Schneider 1927, Anonymous 1929, Hall 1932).

H. collusor, the species predominant in the southwest, breeds mainly in cultivated sandy soils that contain some organic matter. In the Coachella Valley some gnat-producing areas are adjacent to residential areas, but many heavy gnat-producing areas are located 1 to 5 miles or more from populated sections. It is from these cultivated areas that a majority of the pestiferous eye gnats are believed to fly into the residential areas, school yards, etc., to plague residents and tourists alike.

In a current control program, which consists of treatment of the breeding grounds with residual insecticides (Mulla 1958), an important consideration is the distance that the treatment perimeter should be extended from residential areas. It is also necessary to establish the directions in which the gnats generally fly from their centers of high population density. This study was undertaken to answer these and similar questions in regard to flight range, dispersal patterns and rates, population densities, and resting habits.

[1]Paper No. 1135, University of California Citrus Experiment Station, Riverside, California. Accepted for publication February 16, 1959. These investigations were supported by a grant from the Coachella Valley Mosquito Abatement District, Riverside County, California.

[2]The assistance of Leonard D. Moore, Gerry L. Latham, Arthur L. Cavanaugh, and Bart Williams of the Coachella Valley Mosquito Abatement District is greatly appreciated.

MATERIALS AND METHODS

Two 10 mc. shipments of radioactive phosphorus (P^{32}) in the form of $PO_4\equiv$ in weak HCl solution were obtained. The acidic radioisotope solutions were neutralized with equivalent amounts of sodium bicarbonate and diluted to a final volume of 10 ml.

The gnats were labeled by feeding the radioisotope in the following solution: 10 ml. of radioisotope solution and 25 ml. of food solution containing 6 g. human whole blood, 6 g. MRT protein hydrolysate, 12 g. honey, 25 ml. decomposing egg bait (4 eggs in water to make one quart of bait), and 150 ml. water. The 35 ml. of solution was absorbed on four 4-inch lengths of ½-inch thick absorbent dental roll, split lengthwise for maximum feeding surface. All four food rolls were suspended from the top of the feeding cage and exposed to the confined gnats simultaneously. Water was also provided for the confined gnats. In the Palm Desert area, two lots of gnats were fed on succeeding days on the same rolls. After feeding of the first lot, the dental rolls, which were dry but still retained some of the radioisotope, were resoaked in 35 ml. of the food solution and exposed to a second lot of gnats that were released the second day.

The gnats fed readily on the food rolls in each experiment and consumed all the visible traces of food within 2 hours. The gnats were sampled at intervals and checked for radioactivity. After 3 hours of feeding, more than 99 percent of the gnats were labeled. A total period of 5 hours of feeding was allowed for the lots released in the Palm Desert area, however, and of 6 hours for the lot released in the Indio area. The gnats in the Indio area were kept in the feeding cage overnight and released the next morning.

Gnats for labeling were captured either by Tinkham bait traps (four raw eggs in water to make a quart of bait) or by sweeping with nets from around a human face. Since observations have indicated that female gnats are the only ones trapped by both of these operations, it is assumed that only females were captured here

and tagged for flight studies. The gnats were measured volumetrically and their number estimated.

Two releases of labeled gnats were made in the Palm Desert area. The first lot (30,600 gnats) was released at 6:00 p.m. on August 27, 1957, and the second (33,700 gnats) on the following day at the same time. Both releases were made in an alfalfa field where heavy populations of eye gnats prevailed.

Table 1.—Distribution of positive traps (with radioactive gnats) in the Palm Desert area at various collection intervals after release of P^{32}-labeled eye gnats.

Collection no.	Days after first eye gnat release	Total number of traps	
		Positive first time	Containing labeled gnats
1	1	30	30
2	2	7	34
3	4	5	28
4	7	3	35
5	9	2	31
6	11	1	30
7	13	1	26
8	15	0	14
9	17	0	10
10	20	0	8
11	22	0	3
12	25	0	3[a]

[a]These three traps were within ¼ to 1 mile from the release point.

The Palm Desert area is surrounded by high, barren mountains on the east, southeast, south, and southwest. Virgin desert borders this area along its entire northern expanse. The agricultural land is principally composed of date gardens, citrus groves, vineyards, and alfalfa fields. The area includes the main residential and business sections of Palm Desert and Rancho Mirage, as well as farm residences, packing installations, and golf courses.

In the Indio area a single lot (38,000 gnats) was released at 10:00 a.m. on October 10, 1957, in a citrus grove, a typical eye-gnat resting and breeding place. The area surrounding this spot represents a typical intensively farmed section of the Valley, where eye gnats are produced in large numbers as a result of normal farming practices. Observations on tagged gnats during the night were made in this area and some of their resting places determined.

Gnat traps baited with raw egg bait were placed throughout the flight study areas prior to the releases. The frequency of trap collection after release depended upon the weather and the day of the week. Traps were collected more frequently immediately after release and when the weather was calm and hot, under which conditions trap collections are heavier than when the weather is otherwise.

In the Palm Desert area, 12 bait trap collections were made. All traps were checked for labeled gnats at each location. Collections were made on both the first and second day following the first release. Thereafter, seven collections were made at 2-day intervals and three at 3-day intervals. For the first five collections quantitative determinations of the actual numbers of labeled gnats were made for each trap positive for radioactive gnats, and the numbers of unlabeled gnats were estimated volumetrically. After the fifth collection only qualitative determinations were made, the traps being indicated as positive or negative.

In the Indio area 14 collections were made. Two collections were made on the day of release and one the following day. Subsequent collections were made at intervals of 1 to 6 days, depending on weather conditions. When a trap captured labeled gnats for two or three collections, it was discontinued. All traps were negative in the final three collections and the experiment was terminated. The traps in the Indio area were more widely separated than those in the Palm Desert area, and the traps closest to the release

Table 2.—Numbers of labeled and unlabeled eye gnats caught per bait trap in the Palm Desert area over a period of 9 days following the first release of labeled gnats.

Collection no.	Day of collection following first release	Total No. of positive traps	Gnats per trap[a]		Radioactive Gnats per trap[b]	
			Average no.	range	Average no.	Range
1	First	30	1780	22–8000	7.8	1–71
2	Second	34	1900	32–7120	8.5	1–48
3	Fourth	28	1870	100–6800	7.1	1–44
4	Seventh	35	4940	50–23000	11.2	1–47
5	Ninth	31	4590	80–14600	5.4	1–27

[a]Actual counts of gnats were made if the collection was 100 or less. Numbers of gnats over 100 were measured volumetrically.

[b]Actual numbers of radioactive gnats were determined for each trap.

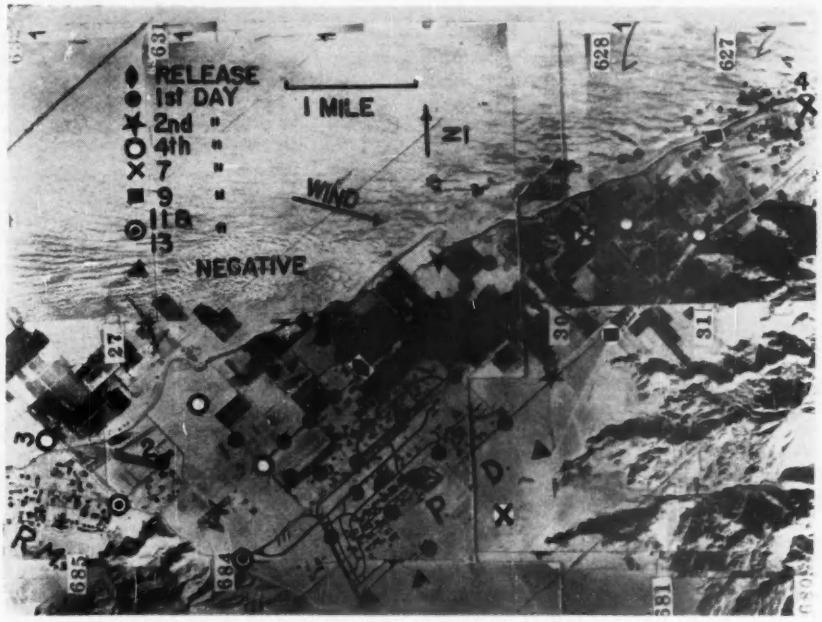


FIG. 1.—Distribution and location of positive and negative eye gnat traps in the Palm Desert area in relation to the point of release of P^{32}-labeled gnats.

point were, therefore, checked first. When a trap was positive for labeled gnats, three to four additional traps were checked beyond the positive trap. However, once a week all the traps were collected, regardless of the dispersion of the tagged gnats. No attempts were made in this experiment to determine the actual number of tagged gnats in each positive trap. Only qualitative determinations were made, the traps being recorded as positive or negative.

RESULTS AND DISCUSSION

Palm Desert Area.—From the nature of the terrain and the location of the residential community in relation to agricultural land, the Palm Desert area offered an ideal combination of conditions for study of the flight range of the eye gnat. This area, as can be seen from the map (fig. 1), is isolated by physical barriers from other areas of the valley except on the west side, where the agricultural section is continuous with the community of Rancho Mirage.

Two releases were made in this area to study the influx of eye gnats from cultivated farms into business and residential areas. The air temperature at the time of release was 98° F. on the first day and 95° F. on the second day. On the first day there was a slight intermittent northwest breeze (3–5 miles/hour) and on the second day the breeze from the same direction was stronger (5–10 miles/hour) until late at night. On the following two days, there were intermittent winds having low velocities (3–10 miles/hour). For the remainder of the experiment the weather was calm and hot (maximum temperatures 95°–112° F.) and favorable for gnat activity.

Of the 52 bait traps set out, 49 caught tagged gnats and 3 remained negative for the duration of the experiment (fig. 1). Of the positive traps, 5 were positive for 10 to 12 collections; 14, for 7 to 9 collections; 14, for 4 to 6 collections; and 16, for 1 to 3 collections. The distribution of traps becoming positive for the first time at various collection intervals after release is shown in table 1. More than half of the traps caught labeled gnats on the day following the first release. After the first day the total number of new traps that caught tagged gnats at each collection decreased rapidly. However, the total number of positive traps remained high (26–35) for a period of 13 days. After 13 days the number of positive traps gradually declined; after 25 days the experiment was terminated.

The labeled gnats dispersed over an area of 4+ square miles within a period of active flight of 5–6 hours. (Gnats are inactive at night and maximum flight activity is noticed early in the morning and late in the afternoon.) After 13 days they had dispersed over about 10 square miles, an expanse representing approximately the total favorable habitat in this area.

From the data presented in table 1, certain

Table 3.—Population density of the eye gnat *Hippelates collusor* (Townsend) calculated from trap collections of labeled and unlabeled gnats in the Palm Desert area.

Day of collection following first release	Total no. of gnats caught in positive traps	Total no. of radioactive gnats	Total gnat population (calculated)	Area surveyed (acres)[a]	Density of gnat population (gnats/A.)
First	53,200	234	7,000,000	2650	2640
Second	64,400	289	14,300,000	3990	3580
Fourth	52,300	200	16,800,000	4860	3450
Seventh	172,800	392	28,400,000	5500	5150
Ninth	142,200	166	55,100,000	5930	9300

[a]Area determined by a planimeter utilizing an aerial photograph of the study area.

reasonable deductions can be made regarding the longevity of eye gnats in the field. Since over half of the traps caught tagged gnats for 13 days following release, it seems reasonable to conclude that the average life span of female eye gnats is greater than 2 weeks and that appreciable numbers may live for 3 weeks or more, considering that the gnats were field-collected and of mixed ages prior to labeling and release.

The numbers of labeled and unlabeled gnats caught per trap in the first five collections are presented in table 2. Traps with high total catches usually caught a greater number of labeled gnats than those with low catches. Traps located in the agricultural areas and adjacent residential sections usually caught large numbers of both labeled and unlabeled gnats. This suggests that eye gnats predominantly fly in the general direction of their natural habitat (see also the distribution and location of positive traps in this study area in figure 1). The negative traps located in barren land at the south end of the main residential section did not attract appreciable numbers of gnats, thus indicating that gnat flight in the direction of nonagricultural and nonresidential areas was at a minimum. A variety of stimuli (physical, chemical, and biological), including those arising from the presence of farmland and residences, influence eye gnat movements.

The majority of the traps located east of trap 1 (see fig. 1) caught medium to large numbers of gnats. Traps 2 and 3, located in proximity to a farming area, also caught well. Trap 4, located 4.1 miles from the point of release, caught few gnats. This was to be expected in view of the fact that the location of this trap was away from agricultural areas and in proximity to few residential quarters surrounded with virgin desert and dry hills. Labeled gnats traversed half a mile of virgin desert from the vicinity of trap 1 to traps 2 and 3. Trap 2 compared favorably with other traps in catch of labeled gnats but did not catch high numbers of unlabeled gnats. Thus it is apparent that the gnats may cross an unfavorable habitat to reach a favorable one on the other side.

Population Density.—From the number of labeled gnats released and the total numbers of labeled and unlabeled gnats captured, it is possible to estimate (table 3) the population density of eye gnats in the Palm Desert area. These approximations involve a number of uncertainties, including mortality of labeled gnats after release and dispersal of gnats outside the area sampled. The estimate of the population density from data on the first day's collection is undoubtedly low as a result of incomplete mixing of the labeled and unlabeled populations. That for the ninth day is undoubtedly high as a result of natural mortality and dispersion beyond the area under study. (See also decrease in average number of labeled gnats per trap on ninth day, table 2.) Estimates for the second, fourth, and seventh days are relatively uniform and seem to be reasonable approximations for the whole area. Gross observations have indicated that a great part of the total female gnat population is confined to one-third to one-fourth of the total area under study. Population density based on the area of the preferred habitat of the gnat would therefore be higher than the average density for the whole community.

Indio Area.—Weather conditions following the release of gnats in the Indio area were unusually inclement. Cool, windy weather prevailed throughout the duration of the experiment. Gnat activity is appreciably reduced by winds over 4 to 5 miles per hour. Cloudy skies and scattered showers (total precipitation of 0.70 inches) occurred during most of the 3-week experimental period. Maximum daily temperatures during the most part of this study remained 67°–94° F. Thus flight activity of the gnats was considerably reduced and some mortality was undoubtedly caused by the substantial precipitation. Despite these adverse conditions, the gnats followed a dispersal pattern similar to that for the Palm Desert area. However, the initial rate of dispersal in the Indio area was slower than that in

the Palm Desert area, the first positive traps being found 3 days after the release of labeled gnats. The ratio of positive traps to negative traps was also considerably less in the Indio area: of 54 bait traps set out, only 17 captured tagged gnats. This low ratio of positive to negative traps may be due in part to the greater spread of traps in this area.

The distribution and location of positive and negative traps is indicated on an aerial photograph of the study area (fig. 2). Dispersal of gnats from the point of release was primarily through the surrounding agricultural area, consisting of frequently irrigated and cultivated date gardens, citrus groves, and truck and field crop plantings. Positive collections were obtained in a trap between two new subdivisions in the town of Indio (Section 559 on the map) to the northeast, but no labeled gnats were detected in any of the traps (only one of a number of traps shown in figure 2) in the residential area of La Quinta to the west. The gnats did not fly in appreciable numbers to the area to the northwest, which is virgin desert except for a few acres of farm land that are not cultivated frequently.

The greatest distance traversed by the gnats in this experiment was 4.3 miles from the point of release. This spot (landmark 46) is located in an environment continuous with that of the release point. All the traps which captured tagged gnats were located either in agricultural land or in residential area.

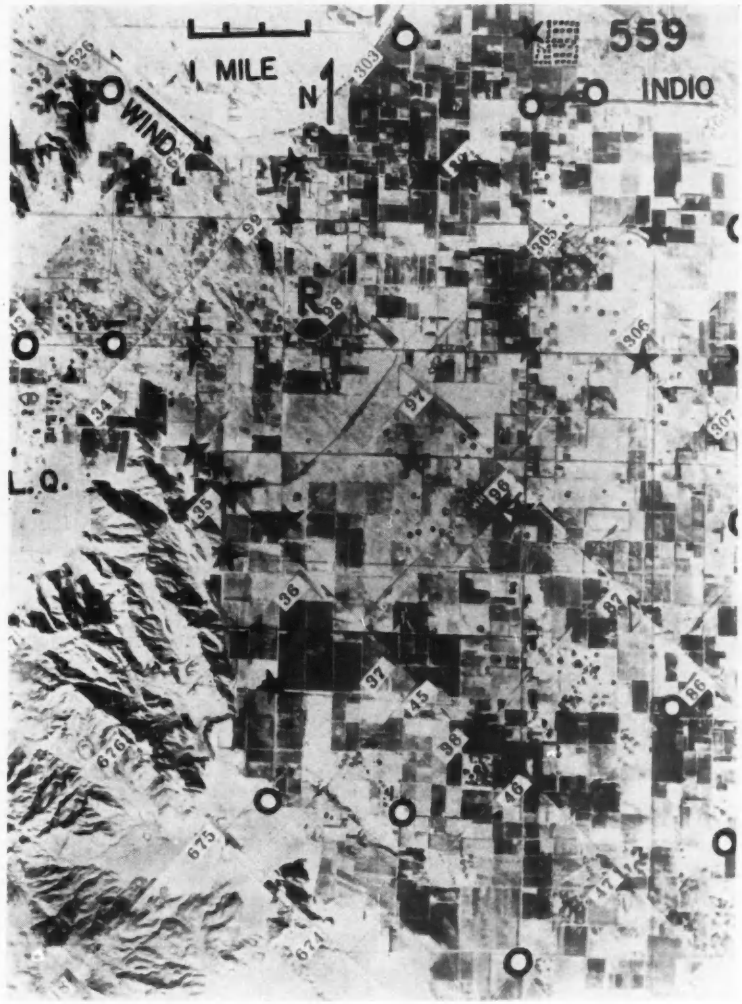


FIG. 2.—Distribution and location of positive (stars) and negative (circles) traps in the Indio area in relation to the point of release (R) of P^{32}-labeled gnats.

A breakdown of the numbers of positive collections on various days during the study period is as follows: 3rd day after release (2 positive collections), 5th (5), 7th (3), 8th (1), 9th (2), 13th (1), and 16th (3). The most distant positive trap was found on the fifth day after release. This trap remained positive for three consecutive collections and was then discontinued.

Resting Places.—Previous attempts to locate gnat resting places at night were unsuccessful. Results of inspections of the trunks and foliage of trees and shrubs and of the litter under the trees were negative. After the release of the labeled gnats in a citrus grove in the Indio area, inspections were made by means of portable Geiger-Müller survey meter on the night following release. The presence of tagged gnats near the surface of the ground was readily ascertained. Further search by flashlight and radiation detection instruments demonstrated that gnats were individually resting on the foliage of low-growing plants, especially broad-leaved species. They were also found on the surface of damp and dry soil, and on dirt clods and dried vegetable matter.

Inspections were also made in a recently cultivated date garden with no vegetation except clumps of Bermuda grass at the base of the date palms. Here the gnats were easily observed on the surface of the dry soil, clinging to clods and dry rootlets protruding above the surface. The distribution of gnats was sparse and at random, and no colony or group of gnats was observed in any single spot. Results of inspections of the Bermuda grass and trunks of the date palms were negative.

REFERENCES CITED

Anonymous. 1929. The California eye gnat. Science 69(1783): XIV.

Hall, D. G., Jr. 1932. Some studies on the breeding media, development and stages of the eye gnat *Hippelates pusio* Loew (Diptera—Chloropidae). Amer. Jour. Hyg. 16(3): 854–64.

Herms, W. B. 1926. *Hippelates* flies and certain other pests of the Coachella Valley, California. Jour. Econ. Ent. 19(5): 692–5.

Mulla, M. S. 1958. Recent developments in the biology and control of Hippelates eye gnats. Proc. and Papers 26th Ann. Conf. California Mosquito Control Assn., Inc. 1958: 78–82.

Schneider, A. 1927. An introductory report on pseudotrachoma endemic in the Salton Sea Region of California. Med. Sentinel 35(3): 154–61.

LES MOUSTIQUES DE L'AFRIQUE DU NORD ET DU BASSIN MÉDITERRANÉEN. LES GENRES CULEX, URANOTAENIA, THEOBALDIA, ORTHOPODOMYIA ET MANSONIA, by G. SENEVET and L. ANDARELLI. Encyclopédie Entomologique, Série A, XXXVII, 383 pp. 1959.

This is the second of a series of three volumes dealing with the mosquitoes of North Africa and the Mediterranean region. This volume covers all of the Culicinae, the Anophelinae having been treated in the first volume and the *Aedes* being reserved for the last. The first part treats the antomy of the culicine mosquitoes, the second part, of 286 pages, describes the 35 species in detail, with keys to the species and descriptions of all known stages and notes on biology. The final part gives detailed distribution records for all of the species.

This is a valuable contribution to our knowledge of mosquitoes of the southern Palaearctic Region. The work is well illustrated but it is unfortunate that the figures for each species are scattered through the text so that for most of the species they are to be found on 5 or more pages, up to 12 pages for two of the species, without any figure references given with the treatment of the species.

One unfortunate error is in the dating of the name *Culex fatigans* Wied. On page 174 this is given as 1820, giving the impression that it precedes *Culex quinquefasciatus* Say, 1823, and on page 187 the date is 1928. The correct date is 1828 and since *C. quinquefasciatus* has a five year priority, *C. fatigans* is actually a synonym. There is also a minor error in the "errata" since p. 39 should be p. 38.

ALAN STONE,
Entomology Research Division,
U. S. Department of Agriculture

AN INTRODUCTION TO THE BEHAVIOR OF INVERTEBRATES, by J. D. CARTHY. 380 pp., 148 figs. The Macmillan Company, New York, 1958. Price, $8.00.

This new book is by Dr. J. D. Carthy, a lecturer at the University of London, who also is author of *Animal Navigation*. True to its title, this book deals with sense organs and the behavior correlated with their function. Emphasis is on behavior rather than anatomy, though many illustrations of anatomical structures occur. Insect behavior is presented amid a broad perspective created by accompanying discussions of other invertebrates. While a simpler and more concise picture of sensory organs and their functions among insects probably is available in Wigglesworth's *Insect Physiology*, or in the revised *Textbook of Entomology*, by Imms, the discussions by Dr. Carthy with constant comparison with other invertebrates should be very useful to many students and investigators.

In addition to a Subject Index, there is a Species Index in which all animals treated, from Protozoa to echinoderms (plus a few vertebrates), are listed with page numbers which pertain to them. Space devoted to insects and non-insects seems to be about evenly divided. In the Bibliography of 591 titles a high percentage of the authors cited are European, though American writers such as Crane, Dethier, Frings, Minnich, and Slifer are well represented.

Among the interesting observations noted is the opinion that insects have the best developed vision except for birds and primates (p. 102), and that among invertebrates only insects have a clearcut ability to detect sound (p. 21).

ASHLEY B. GURNEY,
Entomology Research Division,
U. S. Department of Agriculture

A NEW SPECIES OF APHID ON SUGAR MAPLE (APHIDAE: HOMOPTERA)[1]

CLYDE F. SMITH
Department of Entomology, North Carolina State College, Raleigh

ABSTRACT

Drepanaphis **simpsoni,** on *Acer saccharum* in Canada and the northeastern United States is described and compared with *D. acerifoliae* Thomas.

This new species was first observed by the author in some material that Mrs. M. E. MacGillivray sent for identification from Canada. D. Hille Ris Lambers and G. W. Simpson collected the same species at Presque Isle, Maine, and Hille Ris Lambers also recognized it as an undescribed species. In correspondence of June 2, 1958, he requested that I describe this species, and he suggested that it be named *simpsoni* in honor of Dr. G. W. Simpson, who is presently head of the Department of Entomology at the University of Maine, Orono. This I am pleased to do.

This species is easily recognized because the dorsal abdominal tubercles I, II, and III are all digitate (in most species tubercle III is broadly joined at the base) with tubercle I tending to be the longest. Tubercle I is very dark and unicolorous, a condition which is normally encountered in tubercle III in other species of *Drepanaphis*. The unguis of *simpsoni* is also relatively short for species in this genus.

D. simpsoni differs from *D. acerifoliae* Thomas, the species with which it is most likely to be confused, in tubercles I being dark, unicolorous, and distinctly darker than III, whereas in *acerifoliae* tubercles I and II are dark only on their tips and are distinctly lighter than III. Tubercles III are fused for approximately one-third of their length in *acerifoliae*, whereas in *simpsoni* they are more digitate, being completely separate or only slightly fused at the base (See figs. 1–4).

Drepanaphis simpsoni Smith, new species

Alate vivipara: Color[2] of living material, "Head and thorax roe-brown with very fine white longitudinal lines, abdomen light greenish-yellow with very fine intersegmental wax dots; the anterior pair of tubercles dark only." Cleared specimens show the following characteristic colorations: dusky brown to fuscous on head (except five narrow, longitudinal stripes), thorax, antennal segments I and II, joints of antennae, area around sensoria on antennal VI, tip of fore femur and basal joint of fore tibia, all of abdominal tubercles I, II, III, and IV (tubercle I being unicolorous and slightly darker than other tubercles, color of tubercles II–IV may fade out and be slightly lighter towards base), and sclerites on sides of abdomen cephalad of cornicles. Remaining areas of the body and appendages light (including five narrow longitudinal stripes on head). Wing veins without dusky borders, except base of radius and tips of veins, which are dusky.

Measurements: Body length, 2.05[3] (1.55–2.24); across eyes, 0.52 (0.45–0.54); antennal III, 0.75 (0.75–0.82); IV, 0.53 (0.53–0.62); V, 0.45 (0.45–0.56); VI, 0.13 (0.11–0.15) plus 0.85 (0.78–0.85); rostral IV plus V, 0.08 (0.07–0.09); width, 0.06 (0.06–0.07); hind tibia, 0.93 (0.93–1.04); hind tarsi, 0.12 (0.11–0.14); dorsal tubercle I, 0.19 (0.19–0.24); II, 0.12 (0.08–0.14); III, 0.13 (0.13–0.16); IV, 0.09 (0.07–0.10); cornicles, 0.18 (0.17–0.21); cauda length, 0.11 (0.10–0.11).

Antennal III with 12 (7–14) sensoria; antennal VI with 4 accessory sensoria around primary sensorium; apex of rostrum between 1st and 2nd coxae.

Types: Holotype in the collection of D. Hille Ris Lambers, Bennekom, Netherlands; paracolonotypes[4] in the collections of Hille Ris Lambers, North Carolina State College, and the author. Paratypes in the collections of Mrs. M. E. MacGillivray, G. W. Simpson, and the author.

Type locality: Presque Isle, Maine.

Collections: On *Acer saccharum*, Presque Isle, Maine, September 10, 1956 (Simpson and Hille Ris Lambers), 17 slides containing 33 alate vivipara, October 9, 1958 (Simpson), 6 slides containing 6 specimens; on *Acer* sp., Fredericton, Canada, September 21, 1956 (R. P. Spicer), 5 slides containing 5 specimens; August 28, 1950, 1 slide, 1 specimen (S. E. Vass); 1957, 2 slides, 2 specimens (R. S. Forbes).

[1]Contribution from the Department of Entomology, North Carolina State College, Raleigh, N. C. Published with the approval of the Director as Paper No. 989 of the Journal Series. Accepted for publication February 3, 1959.

[2]Notes on color of living material were furnished by Hille Ris Lambers.

[3]Measurements in millimeters; first measurement is that of the type specimen, measurements in parentheses indicate variation.

[4]Paracolonotypes: specimens collected at the same time as the holotype, usually collected from the same colony.

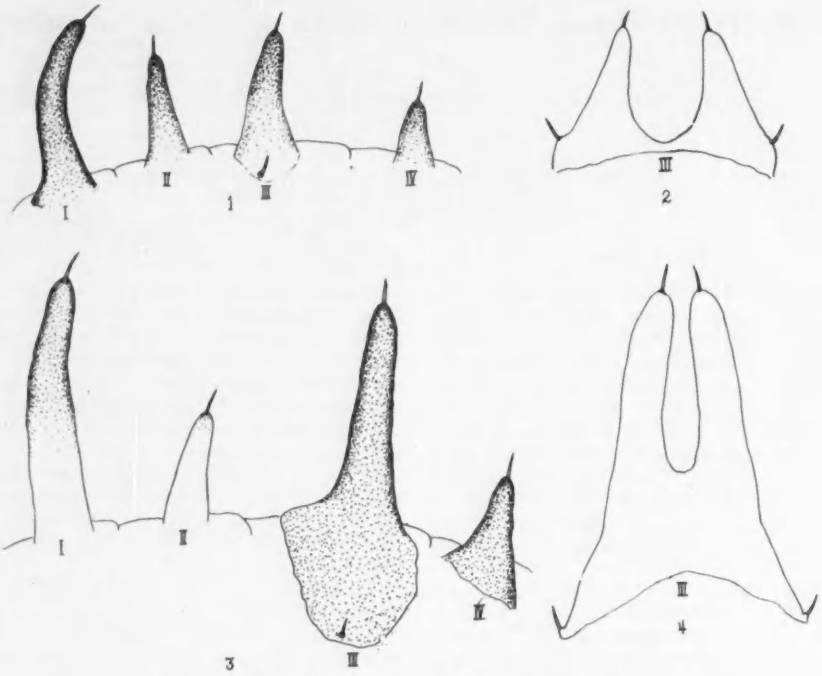


FIG. 1.—*D. simpsoni* Smith, lateral view of abdominal tubercles I–IV.
FIG. 2.—*D. simpsoni* Smith, caudal view of abdominal tubercle III.
FIG. 3.—*D. acerifoliae*, lateral view of abdominal tubercles I–IV.
FIG. 4.—*D. acerifoliae*, caudal view of abdominal tubercle III.
Figures drawn by A. T. Olive.

Since this manuscript was accepted for publication the following collections have been seen from *Acer saccharum*: Windsor, Conn., September 15, 1958, (J. H. Kring, 9 specimens); State College, Pa., July 30, 1959, (C. F. Smith, C. K. Smith, N. Tuatay, B. F. Coon, 2 specimens); Ithaca, N. Y., August 1, 1959, (Smith, Smith, and Tuatay, 1 specimen); Presque Isle, Maine, July 14, 1959, (Smith, Smith, Tuatay, and Simpson, 34 specimens); New Castle, Ontario, Canada, August 2, 1959, (Smith, Smith, and Tuatay, 40 specimens); Ottawa, Ontario, Canada, August 6, 1959, (Smith, Smith, and Tuatay, 23 specimens); Fredericton, New Brunswick, Canada, July 10, 1959, (Smith, Smith, Tuatay, and MacGillivray, 9 specimens).

Alate male: Cleared specimens show the following characteristic colorations: dusky brown on head, thorax, antennals I and II, antennal joints, area around sensoria on antennal VI, tip of fore femora and tips of tarsi, all of cornicles, sclerites on sides of abdomen cephalad of cornicles; dark transverse bars on dorsum of abdomen (especially segments III, IV, V). Wing veins without dusky borders except base of radius and tips of veins which are dusky. The remaining areas of the body and appendages light (including longitudinal stripes on the head).

Measurements: Body length, 2.20 (1.50–2.20); across eyes, 0.58 (0.40–0.58); antennal III, 0.85 (0.72–0.94); IV, 0.60 (0.49–0.60); V, 0.50 (0.41–0.50); VI, 0.13 (0.11–0.13) plus 0.80 (0.66–0.80); rostral IV plus V, 0.08 (0.07–0.08); hind tibia 1.12 (0.88–1.12); hind tarsi 0.15 (0.12–0.15); dorsal tubercles very small, inconspicuous; cornicles 0.17 (0.17–0.18).

Antennal III with 90± sensoria; IV, 70± V, 35±.

Types: Allotype on slide with holotype and one paracolonotype; paracolonotypes of males on slides with paracolonotypes of alate vivipara in the collections of Hille Ris Lambers and the author; paratypes in the collections of Simpson and the author.

Collections: On *Acer saccharum*, Presque Isle, Maine, September 10, 1956 (Simpson and Hille Ris Lambers), 4 specimens on 4 slides; October 9, 1958, 11 specimens on 5 slides (Simpson).

Apterous ovipara: Cleared specimens, faintly dusky on edges of antennal I, antennal joints,

around sensoria on antennal VI, tips of tarsi, marginal sclerites, antesiphuncular sclerite, and sclerites at base of hairs on dorsum of abdomen.

Measurements: Body length, 2.50–2.84 across eyes, 0.55–0.57; hairs slightly fan-shaped at tip on head and body; hairs on vertex of head, 0.12; hairs on dorsum of abdomen, 0.12; antennal III, 0.72–0.78; IV, 0.55–0.56; V, 0.52–0.57; VI, 0.11–0.12 plus 0.72–0.80; rostral IV plus V 0.07–0.08; width, 0.06–0.07; hind tibia 1.14–1.17; hind tarsi 0.14–0.15; cornicles 0.18–0.20.

Antennal III without sensoria.

Types: Paratypes in collections of Hille Ris Lambers, Simpson, and the author.

Collections: On *Acer saccharum*, Presque Isle, Maine, Sept. 10, 1956, (Simpson and Hille Ris Lambers), and October 9, 1958 (Simpson).

NEW ERIOPHYID MITES[1]

H. H. KEIFER[2]

ABSTRACT

A key to *Trisetacus* includes *T.* **grossmanni,** which damages Sitka spruce in Germany, and the three previously known species. *Aceria* **fagerinia,** from Pennsylvania, yellow erineum on beech. **JOHNELLA** includes *J.* **virginiana** from Virginia and *J.* **chrysolepis** from California, both found on oaks. New species from Maryland are: *Cecidophyes* **lyrata,** a leaf vagrant on *Quercus lyrata*; *Aculus* **copallina,** on *Rhus copallina*; *Phyllocoptes* **sassafrasella,** on sassafras; *Epitrimerus* **virginiana,** on *Prunus virginiana*; and *Diptacus* **fragarifoliae,** on wild strawberry; from Virginia, *Rhyncaphytoptus* **rubrifoliae** and *Diptacus* **rubra,** both on *Quercus rubra*; and from California, *Epitrimerus* **demissae,** on *Prunus* **demissa.** A key is given to separate *Cecidophyes* and four related genera. **ANOTHOPODA,** type *A.* **johnstoni,** from Australia, redefines the subfamily Nothopodinae.

Trisetacus grosmanni Keifer, new species
Figure 1A

The new species is most closely related to *T. quadrisetus* (Thom.) by the possession of pointed microtubercles. On *quadrisetus* the accessory seta is about 17 μ long, whereas on the new species it is 7 μ long. The microtubercles on the new species are more pointed and there is a short median line on the shield at the rear margin.

Female 225 μ–245 μ long, 60 μ–70 μ thick, wormlike, dull yellow. Rostrum 28 μ long, curved down. Shield 36 μ long, 50 μ wide; median line present as short line at rear of shield; admedian line inversely curving caudad from in front of dorsal tubercle; first submedian just lateral to admedian; some longitudinal lines lateral to dorsal tubercle. Dorsal tubercles 27 μ apart, set well ahead of rear margin; dorsal setae 34 μ long, projecting forward. Anterior shield seta above rostrum base 20 μ long. Forelegs 30 μ long, tibia 4 μ long, with spur and seta, the seta 10 μ long; claw 10 μ long, tapering; featherclaw 8-rayed. Hindlegs 30 μ long, tibia 4 μ long, tarsus 6.5 μ long, claw 10 μ long. Anterior coxae well separated by median ridge, the tubercles bearing the second and third coxal setae in a transverse line. Abdomen with about 80 rings, completely microtuberculate, each microtubercle produced into a small spinule. Subdorsal seta on about ring 14, approximately 22 μ long. Lateral seta 17 μ long, on ring 11; first ventral 34 μ long, on ring 24; second ventral 22 μ long, on ring 41; third ventral 23 μ long, on ring 4 from rear. Accessory seta 7 μ long. Female genitalia 30 μ wide, 20 μ long, coverflap smooth, seta 20 μ long.

Type locality: Germany, Schleswig-Holstein (Forstrevier, Trittau, Forstort Vorwerksbusch). Collected: June 6, 1958, by Dr. H. Franke-Grosmann. Host: *Picea sitchensis* Carr. (Pinaceae), Sitka spruce. Relation to host: the mites damage the buds. Type material: as well as the dry twigs from which the slides were made there are a type slide and four paratypes. Sitka spruce is native on the west coast of North America and grows on the north California coast. Attempts to find the mite in that location have not been successful. The mite may have come over from a European species of spruce. The species is named for the collector.

KEY TO THE SPECIES OF *TRISETACUS*

1. Microtubercles rounded 2
1. Microtubercles pointed 3
2. Anterior shield seta minute; median and admedian lines present in center of shield; living on various pines . . . . . **pini** (Nal.)
2. Anterior shield seta of moderate length; lines curving caudad from dorsal tubercles, but no central shield lines; on *Cupressus macrocarpa* and *C. bakeri* in California . . . . . **cupressi** (K.)

[1]Accepted for publication February 4, 1959.

[2]State Department of Agriculture, Sacramento, California.

3. Microtubercles pointed, sharp; median line present as short dash before rear shield margin; anterior coxae separated by broad ridge; accessory seta about 7μ long; on Sitka spruce in Germany **grosmanni** K.

3. Microtubercles conical, not particularly sharp; median shield line absent; anterior coxae narrowly separated; accessory seta about 17μ long; on various junipers with a holarctic distribution and on *Cupressus sempervirens* in North Africa **quadrisetus** (Thom.)

Aceria fagerinea Keifer, new species

The European species, *Aceria nervisequus* (Can.), that forms an erineum on the leaves of *Fagus sylvatica* L. is described as follows: 130 μ long, no marks on the shield, the dorsal seta is longer than the shield. The new species is over 200 μ long, has central shield lines, the dorsal seta is the shield length. The new species lacks a foretibial seta, a character not mentioned in the description of the European species. The featherclaw of the new species is unusual in having thick rays.

Female 220 μ–250 μ long, 45 μ–60 μ thick, dull yellow in color, wormlike. Rostrum small, 16 μ long, curved down. Shield 27 μ long, 40 μ wide, declivitous; median line and parallel admedians present, interspersed with granules; lateral shield granulations. Dorsal tubercles 25 μ apart; dorsal setae 27 μ long. Forelegs 25 μ long, tibia 4.5 μ long, seta missing; tarsus 6.5 μ long; claw 6 μ long; featherclaw 4-rayed, the rays thick. Hindlegs 22 μ long, claw 9 μ long. Anterior coxae broadly contiguous, an area of granules just within the second setiferous tubercles; second tubercles well ahead of transverse line through third coxal tubercles. Abdomen with about 75 rings, completely microtuberculate, the microtubercles rounded, well spaced, and well ahead of rear ring margin. Lateral seta 18 μ long, on about ring 10; first ventral 25 μ long, on ring 24; second ventral 9 μ long, on ring 44; third ventral 15 μ long, on ring 6 from rear. Accessory seta absent. Female genitalia 21 μ wide, 16 μ long, coverflap with base granular, the rear part smooth; genital seta 12 μ long.

Type locality: Hawley, Pa. Collected: July 1, 1958, by Stanley Mesavage, and forwarded under No. 58–10936 from the USDA Research Service. Host: *Fagus grandiflora* Ehr. (Fagaceae), beech. Relation to host: The mites form upper surface yellow erineum patches. Type material: as well as dry material from which the slides were made, there are a type slide and five paratypes.

Cecidophyes lyrata Keifer, new species

Figure 1B

The new species differs from another congeneric oak infestor, *C. caliquerci* (K.), by having a 4-rayed featherclaw, which is one less ray than on *caliquerci*. The new species is a vagrant on both leaf surfaces on its host and is deep purple in color, whereas *caliquerci* is confined to the upper surface of oak leaves and is a light transparent purple.

Female 200 μ–215 μ long, 55 μ thick, robust-spindleform, deep purple. Rostrum 23 μ long, projecting down. Shield 45 μ long, 45 μ wide, anterior lobe broad and blunt. Design a network of lines of granules: median line present, long, joined to admedians by two cross lines; two distinct submedian lines present on each side, intersected by two curved transverse lines running across shield; lateral granulations present. Dorsal tubercles and setae missing. Forelegs 37 μ long, tibia with seta, claw 7 μ long, slightly tapering, featherclaw 4-rayed. Hindlegs 35 μ long, claw 7 μ long. Anterior coxae somewhat separated by appressed genitalia, narrowly touching on inner lobes, setiferous tubercles somewhat raised, the second tubercles well ahead of transverse line through third tubercles. Abdomen with about 50 tergites and 60 sternites, but not significantly differentiated; rings completely set with rounded microtubercles which touch rear ring margins and are more elongate dorsally. Lateral seta 17 μ long, on sternite 5; first ventral seta 48 μ long, on sternite 17; second ventral 10 μ long, on sternite 36; third ventral 25 μ long, on sternite 5 from rear. Accessory seta absent. Female genitalia appressed to coxae, 24 μ wide, 15 μ long, coverflap with about 16 longitudinal furrows in two uneven ranks; genital seta 10 μ long.

Type locality: Greenbelt, Maryland. Collected: August 19, 1958, by John P. Keifer. Host: *Quercus lyrata* Walt. (Fagaceae), overcup oak. Relation to host: the mites are vagrants on both leaf surfaces. Type material: as well as the dry mites on the leaves, from which the slides were made, there are a type slide and three paratypes.

Jobnella Keifer, new genus

The new genus is allied to *Cecidophyes* by having appressed female genitalia, shortened anterior genital apodeme, and the longitudinal coverflap furrows in two uneven ranks. In common with *Cecidophyes*, the species referable here lack dorsal tubercles and setae. The new genus is characterized principally by having broad tergites, the first of which is united to the rear of the shield, and which extends caudad centrally, dividing the second tergite.

Body spindleform, somewhat flattened dorsoventrally, with a series of broad tergites, narrow sternites, the terminal section of abdomen with narrow rings. Rostrum comparatively large, curving down, chelicerae evenly curved; recurved distal part of oral stylet shorter than base plus pharyngeal pump. Shield subtriangular, with lobe over rostrum; dorsal tubercles and setae missing. Coxae either separated or narrowly joined by centrally projecting lobes; all three pairs of coxal setae present. Legs with all usual setae, the featherclaws simple. Abdomen with seven tergites, all broad except second; first

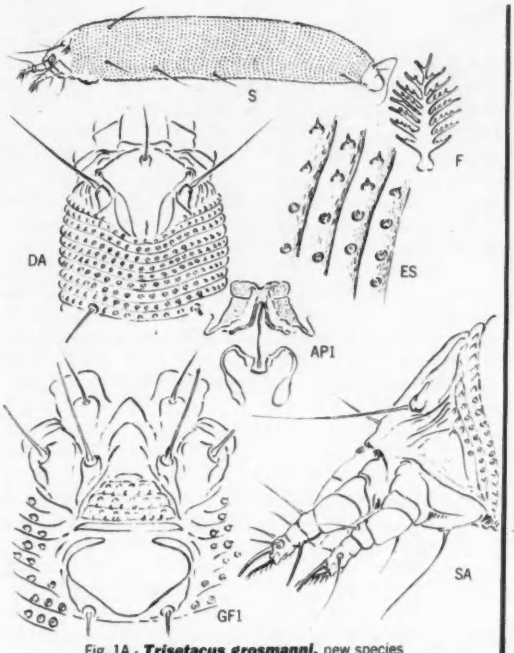


Fig. 1A - ***Trisetacus grosmanni,*** new species

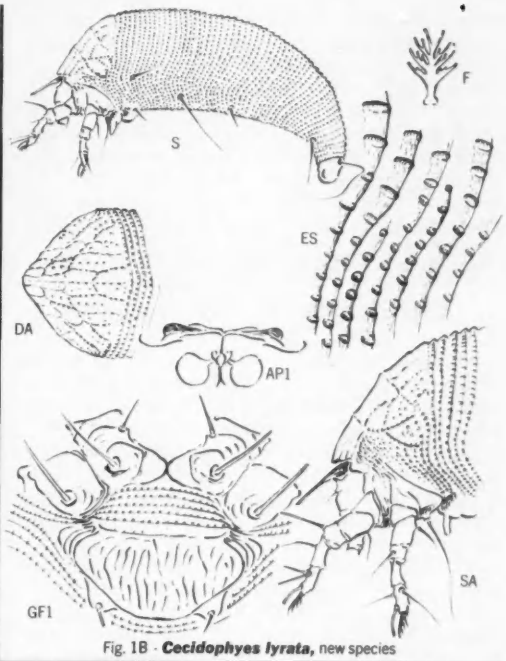


Fig. 1B - ***Cecidophyes lyrata,*** new species

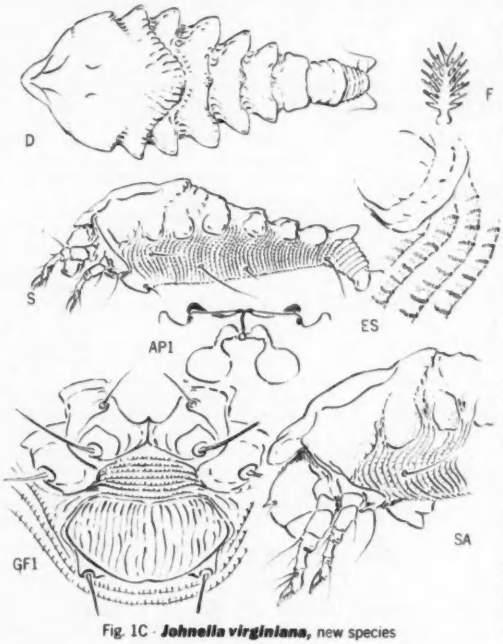


Fig. 1C - ***Johnella virginiana,*** new species

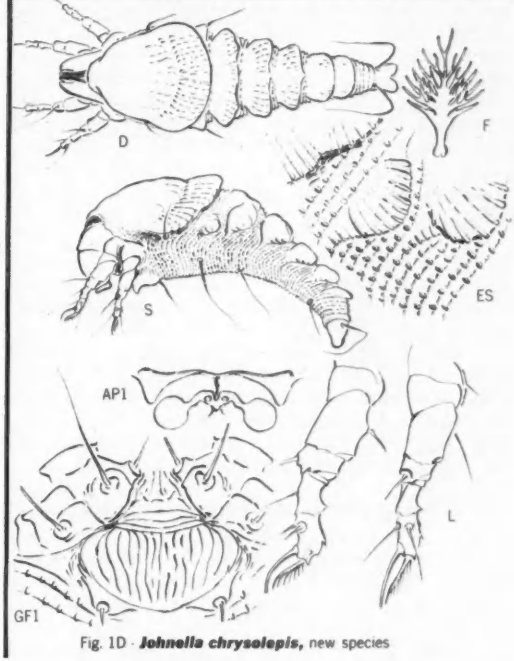


Fig. 1D - ***Johnella chrysolepis,*** new species

API—Interior structures of female genitalia
D—Dorsal view of mite
DA—Dorsal view of shield and adjacent sections
ES—Lateral surface structures
F—Featherclaw, of protogyne and male
FD—Featherclaw of deutogyne
GF1—Female genitalia and coxae
L—Legs on left side
S—Side view of mite
SA—Left side of anterior section of mite

tergite broadly joined to rear of shield and projecting caudad dividing the second tergite; caudal tergite somewhat projecting. Sternites narrow and with elongate microtubercles, the sternites tending to extend dorsally between tergites. Termen of abdomen projecting diagonally down and with narrow rings. Female genitalia appressed to coxae, coverflap with numerous longitudinal furrows, part in two uneven ranks; internal apodeme shortened in ventral view.

Genotype: *Johnella virginiana*, new species.

Johnella virginiana Keifer, new species

Figure 1C

Female 150 μ–160 μ long, 65 μ wide, 45 μ thick, flattened, spindleform, dull whitish. Rostrum large, 30 μ long, curving down. Shield 52 μ long, 55 μ wide, lobe over rostrum of moderate size; a slight longitudinal anterior ridge from center of anterior lobe; center of shield slightly raised. Forelegs 25 μ long, tibia 6 μ long, with seta; tarsus 6.5 μ long; claw 6.5 μ long, somewhat tapering; featherclaw 7-rayed. Hindlegs 23 μ long, claw 6.5 μ long. Anterior coxae narrowly touching by central extensions; first and second coxal tubercles equidistant from center line, second tubercles ahead of line across third tubercles. Abdomen with 7 broad tergites and 45–55 sternites; cauda with about 6 rings; broad tergites without definite sculpturing; narrow sternites set with elongate microtubercles. Lateral seta 14 μ long, on sternite 5; first ventral 33 μ long, on sternite 17; second ventral 11 μ long, on sternite 27; third ventral 24 μ long, on sternite 5 from rear. Accessory seta absent. Female genitalia 22 μ wide, 11 μ long, coverflap with about 24 longitudinal furrows, part in two ranks; genital seta 12 μ long.

Type locality: Williamsburg, Virginia. Collected: September 17, 1958, by John P. Keifer. Host: *Quercus virginiana* Mill. (Fagaceae), live oak. Relation to host: the mites are vagrants among the stellate hairs on the undersurface of the leaves. Type material: as well as the dry material from which the slides were made, there are a type slide and seven paratype slides. The new genus is named for the collector of the genotype, who has also furnished a number of the other new species included in this article.

Johnella chrysolepis Keifer, new species

Figure 1D

This species differs from *J. virginiana* by having the tergites lined with elongate microtubercles, the anterior shield lobe smaller, and the anterior coxae separated.

Female 155 μ–170 μ long, 55 μ wide, spindleform, dull yellowish. Rostrum 31 μ long, curved down. Shield 45 μ long, 50 μ wide, small anterior lobe over rostrum; shield design lacking. Forelegs 28 μ long, tibia 6 μ long, with seta; tarsus 7 μ long; claw 8.5 μ long; featherclaw 7-rayed. Hindlegs 26 μ long, claw 9 μ long, somewhat tapering. Anterior coxae separated, the first setiferous tubercles nearer midline than the second tubercles; all three tubercles on a side in a diagonally outward line. Dorsum of abdomen with seven broad tergites, the first joined to rear of shield. Tergites sculptured with elongate microtubercles. Sternites narrow, with rounded microtubercles. About 63 sternites, including the termen which has 6 small rings. Lateral seta 13 μ long, on sternite 7; first ventral 35 μ long, on sternite 18; second ventral 21 μ long, on sternite 31, third ventral 21 μ long, on sternite 6 from rear. Accessory seta absent. Female genitalia 23 μ wide, 13 μ long, coverflap with about 16 uneven longitudinal furrows; genital seta 28 μ long.

Type locality: Spring Mountain Road, west of St. Helena, Sonoma County, Calif. Collected: August 18, 1957, by H. H. Keifer. Host: *Quercus chrysolepis* Liebm. (Fagaceae), maul oak. Relation to host: the mites are vagrants among the yellow hairs on the undersides of the leaves. Type material: as well as the dry material, there are a type slide and eight paratypes.

The two species in this genus are extreme forms of a series of genera and species that combine the lack of dorsal tubercles and setae with appressed female genitalia and shortened internal apodeme. This combination cuts across conventional classification lines and is an easy group to define. It may eventually be possible to designate a subfamily for this based on the genus *Cecidophyes*. A key to the genera involved is as follows:

1. Shield with no anterior projection, leaving the rostrum fully exposed in dorsal view; body elongate and wormlike; these mites living under cover in all cases . . . . . Eriophyinae: **Cecidophyopsis** K., 1959 (1)
1. Shield with anterior lobe obscuring rostrum at least in part in dorsal view; body more robust and spindleform; species usually living as leaf vagrants . . . . . Phyllocoptinae 2
2. Abdomen completely microtuberculate, with tergites and sternites very similar 3
2. Abdomen with tergites and sternites strongly differentiated laterally, the former much broader . 4
3. Abdomen dorsally rounded . . . . . **Cecidophyes** Nalepa, 1889 (2 and 3)
3. A dorsal abdominal longitudinal concavity present . . . . . **Glyptacus** K., 1953 (4)
4. About 12 broad tergites, the first distinctly separated from shield . . . . . **Coptophylla** K., 1944 (5)
4. Abdomen with seven broad tergites, the first joined to rear margin of shield . . . . . **Johnella** K.

Aculus copallina Keifer, new species

The combination of the 5-rayed featherclaw with rounded microtubercles is definitive, but the most distinct character of this mite is the presence of paired ovals in the shield design at the rear center of the shield. (See reference No. 6 for *Aculus*).

Female 160 μ–170 μ long, 45 μ wide, 40 μ thick,

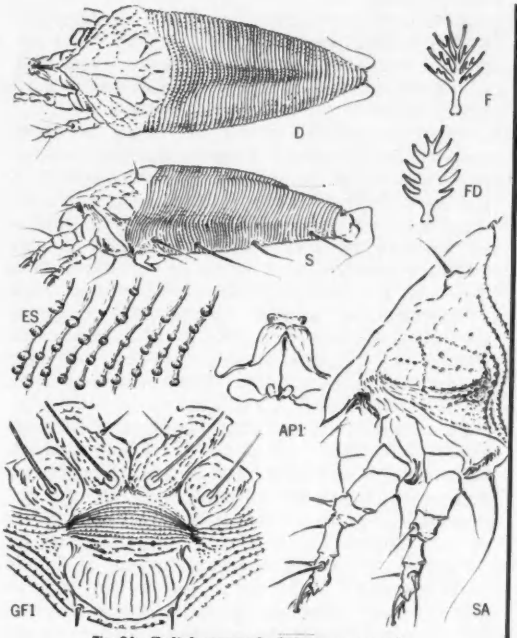


Fig. 2A - ***Epitrimerus virginiana,*** new species

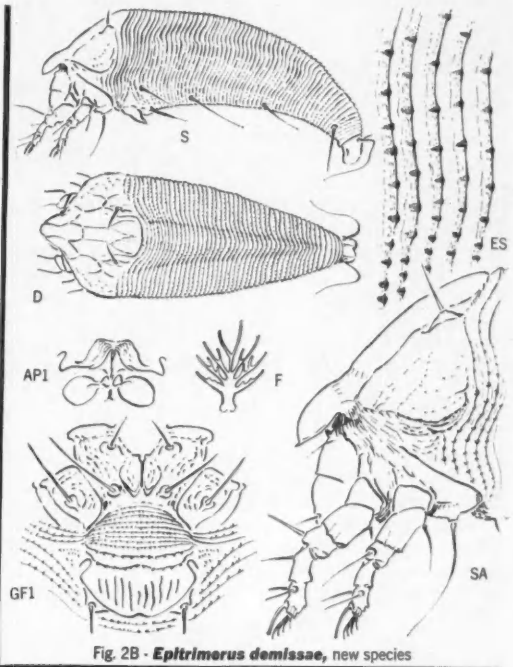


Fig. 2B - ***Epitrimerus demissae,*** new species

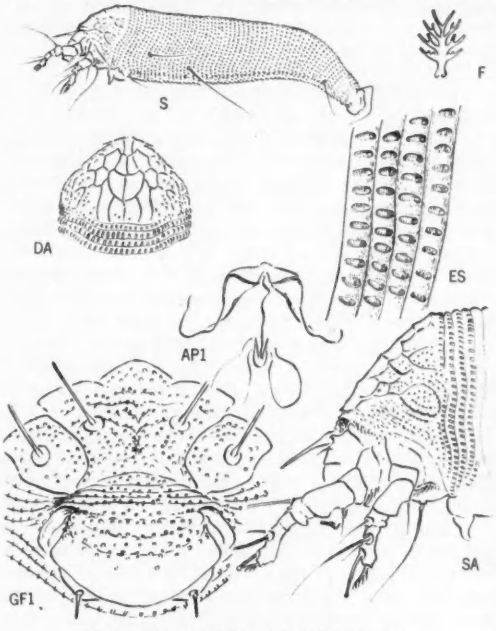


Fig. 2C - ***Anothopoda johnstoni,*** new species

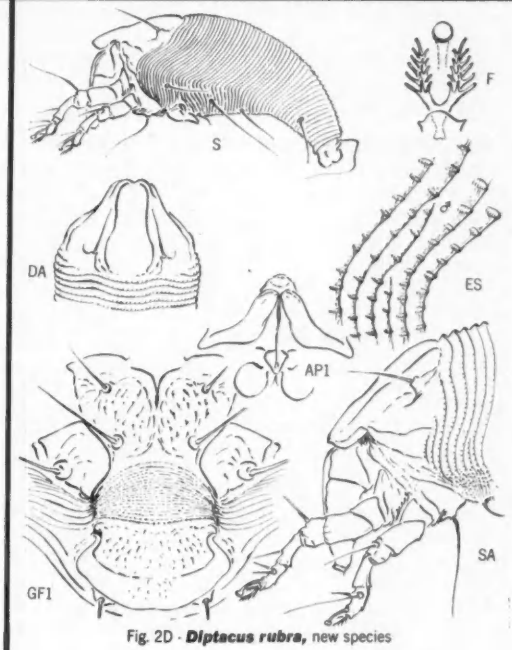


Fig. 2D - ***Diptacus rubra,*** new species

elongate-spindleform, dull reddish. Rostrum 21 μ long, projecting down. Shield 41 μ long, 40 μ wide, anterior lobe pointed. Median line indicated on rear half of shield; admedians complete, undulate, with the median line forming a pair of ovals at the rear margin. First submedians branching from admedians at ¼ and framing the central shield section in an elongate ellipse. Lateral diagonal lines and moderate lateral lobes present, the lobes edged with granulations. Dorsal tubercles 28 μ apart; dorsal setae 18 μ long. Forelegs 31 μ long, tibia with seta, tarsus 6.5 μ long, claw 7 μ long, tapering; featherclaw 5-rayed. Hindlegs 27 μ long, claw 7.5 μ long. Anterior coxae contiguous, with rough curved lines; first and second setiferous tubercles equidistant from median line; second tubercles well ahead of transverse line through third tubercles. Abdomen with about 45 narrow tergites and 65–75 sternites; completely microtuberculate, the microtubercles rounded and somewhat elongate dorsally. Lateral seta on sternite 7, 18 μ long; first ventral 32 μ long, on sternite 23; second ventral 27 μ long, on sternite 52; third ventral 23 μ long, on sternite 4 from rear. Accessory seta present. Female genitalia 20 μ wide, 17 μ long, coverflap with 10–11 longitudinal furrows; genital seta 18 μ long.

Type locality: Greenbelt, Maryland. Collected: August 22, 1958, by John P. Keifer. Host: *Rhus copallina* L. (Anacardiaceae), winged sumac. Relation to host: the mites are undersurface vagrants on the leaves. Type material: as well as the dry leaves from which the slides were made, there are a type slide and three paratypes.

Phyllocoptes sassafrasella Keifer, new species

The most distinct feature of this species is the strong network design on the shield. The anterior shield lobe is pointed and bent down, and the admedian lines, which are very close in front, diverge gradually and regularly to rear. The dorsal microtubercles on the protogyne are conical. This mite does not seem to be very close to any other such species so far seen by the writer.

Female 160 μ–170 μ long, 50 μ wide, 50 μ thick, spindleform, dull reddish in color. Rostrum 25 μ long, projecting down. Shield 40 μ long, 45 μ wide, anterior lobe over rostrum acuminate and bent down. Shield design a network of strong lines: median line distinct on rear two-thirds, joined to admedians by two dart-shaped marks; admedians strong, complete, close anteriorly, gradually diverging to rear margin; first submedian curving and forming cells with the admedian and with lateral lines; lateral part of shield not lobed, bearing a strong network design to shield edge. Dorsal tubercles 18 μ apart, touching rear margin but extending diagonally forward in their long dimension; dorsal setae 13 μ long, directed diagonally centrally and to the rear. Forelegs 30 μ long, tibia with seta, claw 9 μ long, tapering, slightly knobbed; featherclaw 5-rayed. Hindlegs 30 μ long, claw 9 μ long. Anterior coxae contiguous, with lines of granules; an inverse curved line on inner side of each second tubercle. First coxal tubercles a little farther from median line than second tubercle; second tubercles ahead of transverse line through rear coxal tubercles. Abdomen with about 53 tergites and 68 sternites; tergites narrow and completely microtuberculate, the dorsal microtubercles somewhat conical; sternal microtubercles smaller and rounded. Lateral seta 15 μ long, on sternite 9; first ventral 42 μ long, on sternite 24; second ventral 18 μ long, on sternite 43; third ventral 18 μ long, on sternite 5 from rear. Accessory seta present. Female genitalia 20 μ wide, 14 μ long, coverflap with 11–12 furrows; seta 16 μ long.

Type locality: Greenbelt, Maryland. Collected: August 28, 1958, by John P. Keifer. Host: *Sassafras officinale* N. & E. (Lauraceae), sassafras. Relation to host: the mites are vagrants on the undersides of the leaves. Type material: as well as the dry leaves from which the mites on the slides were taken, there are a type slide and six paratypes. The deutogynes of this species were present in some numbers at the time of collection. The tergites on the deutogynes are more similar to the sternites as to width and microtuberculation than is the case on the protogynes. The featherclaws of the deutogyne are similar to those on the protogyne.

Epitrimerus virginiana Keifer, new species

Figure 2A

The lateral shield lobes, sharp anterior shield lobe, and tapering middorsal ridge are defining features of this species. *Epitrimerus pyri* (Nal.) has lateral shield lobes and a similar featherclaw, but the shield design is less distinct and the middorsal abdominal ridge is less prominent and broader. The deutogyne of the new species illustrates the fact that this alternate stage does not necessarily always have the same number of rays in the featherclaw as the protogyne. In this case the protogyne has a featherclaw with 4 slender rays, whereas the deutogyne has a 5-rayed structure with thick rays.

Female 160 μ–170 μ long, 60 μ wide, 45 μ thick, short spindleform, dull yellowish. Rostrum 21 μ long, projecting down. Shield 42 μ long, 50 μ wide, anterior lobe acuminate and sharp; design a network with the lateral lines composed of granules. Median line slightly indicated toward rear of shield and joined to admedians by a dart-shaped mark. Admedians nearly complete, slightly undulating and diverging to rear; first submedian on posterior two-thirds, running diagonally outside of dorsal tubercles, joined to admedians by two transverse lines; lateral network of granules; lateral shield lobes edged with

granules. Dorsal tubercles 24 μ apart, base of tubercles extending ahead from rear margin; dorsal setae 7 μ long, projecting up and central. Forelegs 30 μ long, tibia with seta, claw 6 μ long; featherclaw 4-rayed. Hindlegs 28 μ long, claw 6 μ long. Anterior coxae touching centrally, lined with granules; first tubercles well ahead of second tubercles and farther from midline; second tubercles but little ahead of transverse line through third tubercles. Abdomen with about 43 tergites and 65–70 sternites. Tergites narrow and with middorsal ridge broad at shield edge and tapering to rear one-fourth of abdomen; tergites incompletely microtuberculate, the areas between the ridge and lateral edges of dorsum apparently lacking microtubercles. Sternites completely microtuberculate, the microtubercles rounded, both dorsal and ventral. Lateral seta 20 μ long, on about sternite 10; first ventral 20 μ long, on sternite 26; second ventral 18 μ long, on sternite 47; third ventral 24 μ long, on sternite 5 from rear. Accessory seta present. Female genitalia 21 μ wide, 14 μ long, coverflap with about 14 longitudinal furrows: genital seta 20 μ long.

Type locality: Greenbelt, Maryland. Collected: August 28, 1958, by John P. Keifer. Host: *Prunus virginiana* L. (Rosaceae), choke cherry. Relation to host: the mites live on the underside of the leaves. Type material: as well as the dry leaves from which the slides were made, there are a type slide and eight paratypes.

Epitrimerus demissae Keifer, new species

Figure 2B

The host of this mite is at times designated as a subspecies of the host of the above *Epitrimerus*, so the two species of mites can be compared. The western mite, *demissae*, has a blunt shield lobe, a less distinct shield design, less prominent lateral shield lobes, and a broader dorsal ridge on the abdomen.

Female 165 μ–170 μ long, 50 μ wide, 50 μ thick, spindleform, light dull yellowish in color. Rostrum 23 μ long, projecting down. Shield 50 μ long, 50 μ wide, with an anterior lobe rounded in dorsal view, somewhat acute at lower edge. Median line on shield absent; admedians complete, diverging posteriorly with a curved line from each touching at rear center; partial submedian line ahead of dorsal tubercles; lateral shield design obscure, the lateral lobes not prominent and with some edge granules. Dorsal tubercles 23 μ apart, extending ahead from rear margin; dorsal setae arising ahead of rear margin, projecting up and centrad, 10 μ long. Forelegs 31 μ long, tibia with seta, claw 6.5 μ long, featherclaw 4-rayed. Hindlegs 29 μ long, claw 6.5 μ long. Anterior coxae contiguous less than one-half length, lined with short dashes and with inwardly curved lines inside second tubercles. First coxal tubercles well ahead of second and a little farther from midline; second coxal tubercles but little ahead of transverse line through third tubercles. Abdomen with about 58 tergites and 70 sternites; central dorsal longitudinal ridge narrowing to rear from shield; abdomen completely microtuberculate, these all touching rear ring margins, fainter dorsally, not produced. Lateral seta 20 μ long, on sternite 10; first ventral 45 μ long, on sternite 24; second ventral 20 μ long, on sternite 48; third ventral 25 μ long, on sternite 5 from rear. Accessory seta 4 μ long. Female genitalia 21 μ wide, 12 μ long, coverflap with 10–11 longitudinal furrows; seta 22 μ long.

Type locality: Cedar Pass, northeast of Alturas, Modoc County, Cal. Collected: September 2, 1953, by H. H. Keifer. Host: *Prunus demissa* (Nutt.) (Rosaceae), western choke cherry. Relation to host: The mites rust the undersides of the leaves and the white cast skin streaks are very conspicuous. Type material: as well as the dry mites on the leaves, from which the slides were made, there are a type slide and four paratype slides.

Anothopoda Keifer, new genus

This genus is related to *Nothopoda* K. (7) and to *Floracarus* K. (8), and is referable to the subfamily Nothopodinae (9). The species in these two genera have a united tibio-tarsus which is the principle defining character of the subfamily. The species in the new genus differs in having a reduced but distinct tibia on the foreleg, but with apparently a tibio-tarsus on the hindleg. The other peculiarities of this group, such as the absence of coxal seta number one and the united forecoxae, are present. The new genus is distinguished by lacking the dorsal setae and the second ventral setae.

Body elongate-spindleform, circular in cross section. Rostrum small, chelicerae straight; distal recurved part of oral stylet shorter than base plus pharyngeal pump. Shield declivitous anteriorly, semicircular in dorsal view; no appreciable lobe over rostrum; dorsal tubercles and setae missing. Forelegs with reduced but distinct tibia which lacks a seta; hindlegs with tibio-tarsus; all other usual leg setae present. Anterior coxae broadly fused to each other; first tubercles and setae missing. Abdominal rings about equal dorsoventrally, completely microtuberculate; second ventral setae missing. Female genitalia a moderate distance from coxae; anterior apodeme elongate in ventral view; coverflap lacking longitudinal furrows.

Genotype: *Anothopoda johnstoni*, new species.

Anothopoda johnstoni Keifer, new species

Figure 2C

Female 150 μ–190 μ long, 50 μ thick, elongate, tapering, dull yellowish. Rostrum 17 μ long, projecting down. Shield 27 μ long, 35 μ wide,

design a network: Median line indicated on posterior three-fourths; admedians undulate and joined to median by three cross lines; submedian and lateral lines forming part of a network; shield with lateral granules among lines. Forelegs 27 μ long, tibia 2.5 μ long, lacking seta; tarsus 6.5 μ long; featherclaw 4-rayed. Hindleg 24 μ long, tibio-tarsus 8.5 μ long, claw 6.5 μ long. Coxae granular; second tubercles ahead of transverse line across third tubercles. About 63 abdominal rings; microtubercles elongate. Lateral seta 17 μ long, on ring 10; first ventral 32 μ long, on ring 20; second ventral seta missing; third ventral seta 16 μ long, on ring 7 from rear. Accessory seta absent. Female genitalia 23 μ wide, 14 μ long, coverflap smooth except for basal granules; seta 5 μ long.

Type locality: Burnley, Victoria. Collected: May 7, 1957, by C. J. R. Johnston, for whom the species is named. Host: *Prostanthera lasianthus* (Labiatae), spice bush. Relation to host: these mites occur in leaf erineum and are mixed with *Aceria prostantherae* K. (10). This latter species is probably the erineum-former. Type material: As well as the dry leaves and erineum, from which the slides were made, there are a type slide and four paratypes.

Rhyncaphytoptus rubrifoliae Keifer, new species

The distinctive feature of this mite is that it has a smooth shield with no lines.

Female 200 μ–210 μ long, 50 μ thick, elongate, wormlike, dull yellowish. Rostrum 37 μ long, pointed down. Shield 33 μ long, 38 μ wide, a short broad lobe over rostrum; shield with no markings. Dorsal tubercles 23 μ apart, on rear margin; dorsal setae 27 μ long, directed ahead. Forelegs 36 μ long, tibia 10 μ long, with seta 12 μ long; tarsus 10 μ long; claw 7 μ long, knobbed; featherclaw 7 to 8-rayed. Hindlegs 33 μ long, tibia 6.5 μ long, tarsus 8.5 μ long, claw 8.5 μ long. Anterior coxae with a curved line just inside each second tubercle; first and second tubercles close, the second directly behind first and well ahead of transverse line through third tubercles. Abdomen with about 47 tergites and 55 sternites; completely microtuberculate, the microtubercles on ring margins, blunt, less prominent dorsally. Lateral seta 23 μ long, on sternite 10; first ventral 60 μ long, on sternite 21; second ventral 14 μ long, on sternite 30; third ventral 20 μ long, on sternite 5 from rear. Accessory seta 6.5 μ long. Female genitalia 26 μ wide, 18 μ long, coverflap smooth with an obscure basal concentric line; seta 10 μ long.

Type locality: Virginia Beach, Va. Collected: September 17, 1958, by John P. Keifer. Host: *Quercus rubra* L. (Fagaceae), red oak. Relation to host: the mites are undersurface vagrants. Type material: as well as the dry leaves, from which the slides were made, there are a type slide and two paratypes.

Diptacus rubra Keifer, new species

Figure 2D

The distinctive features of this mite are the broad anterior shield lobe with median indentation, the lack of a median line, the moderately produced dorsal tubercles, the lack of a definite ridge between the forecoxae.

Female 150 μ–160 μ long, 55 μ thick, robust-spindleform, reddish. Rostrum 36 μ long, projecting down. Shield 46 μ long, 47 μ wide, anterior lobe broad, short, with a median indentation. Median line absent from design, but admedians complete and curving back from anterior lobe, framing the center area, the rear part subcircular. Submedian and lateral lines absent except for a line along lateral margin of shield. Dorsal tubercles 28 μ apart, a little ahead of rear shield margin and diagonally placed. Dorsal setae 15 μ long, projecting forward. Forelegs 44 μ long, tibia 12 μ long, with seta; tarsus 8 μ long; claw 6 μ long, knobbed; divided featherclaw 6-rayed on a side. Anterior coxae broadly touching, lined and granular; first coxal tubercle farther from midline than the second; second tubercles well ahead of transverse line through third tubercles. Abdomen with about 46 tergites and a few more sternites; completely set with elongate microtubercles which reach rear ring margins and are blunt and less prominent dorsally. Lateral seta 24 μ long, on about sternite 12; first ventral 60 μ long, on sternite 25; second ventral 16 μ long, on sternite 49; third ventral 30 μ long, on sternite 8 from rear. Accessory seta absent. Female genitalia 30 μ wide, 18 μ long, basal area of coverflap covered with short dashes, otherwise smooth; genital seta 6 μ long.

Type locality: Virginia Beach, Va. Collected: September 17, 1958, by John P. Keifer. Host: *Quercus rubra* L. (Fagaceae), red oak. Relation to host: The mites are vagrants on the underside of the leaves. Type material: as well as the mites on the dry leaves, from which the slides were made, there are a type slide and four paratypes. It is possible that the above description refers to the deutogyne of the species. Collections earlier in the season would determine the correct status of the form figured.

Diptacus fragarifoliae Keifer, new species

This mite is close to *D. gigantorhynchus* (Nal.). It differs in having one more ray on the featherclaw and in having a less prominent ridge between the forecoxae.

Female 215 μ–240 μ long, 80 μ–90 μ thick, elongate-spindleform, yellowish. Rostrum 55 μ long, projecting down. Shield 35 μ long, 63 μ wide, with almost no anterior lobe; design a network: median line complete; admedians complete, joined both to median and submedian lines and curving at the junctions, the admedians turning centrad to rear and forming an acute

angle with median at rear margin; curved submedian line extending back from diagonal line across front of shield and curving inversely in front of dorsal tubercles to end at admedian line; sides of shield with cells formed by lateral lines with included granulations. Dorsal tubercles well ahead of rear shield margin, 22 μ apart; dorsal setae short, 4 μ long, projecting up. Forelegs 42 μ long, tibia 13 μ long, with 9 μ seta ventrally placed; tarsus 8.5 μ long, claw 8 μ long, knobbed; featherclaw 6-rayed on a side. Hindlegs 39 μ long, tibia 10.5 μ long, tarsus 7 μ long, claw 8.5 μ long. Anterior coxae separated by a slight ridge, the coxae with lines of granules; first tubercles well ahead of second tubercles and slightly farther from midline; second tubercles not far ahead of a transverse line through third tubercles. Abdomen with tergites and sternites subequal, about 75–80 in number; completely set with rounded, small, microtubercles which are a little ahead of ring margin and less prominent dorsally. Lateral seta 57 μ long, on about sternite 10; first ventral 70 μ long, on sternite 27; second ventral 45 μ long, on sternite 45; third ventral 40 μ long, on sternite 11 from rear. Accessory seta very short. Female genitalia 28 μ wide, 23 μ long, coverflap smooth except for basal granulations; seta 17 μ long.

Type locality: Greenbelt, Maryland. Collected: August 29, 1958, by John P. Keifer. Host: *Fragaria virginiana* Duchesne (Rosaceae), wild strawberry. Relation to host: The mites are vagrants on the undersides of the leaves. Type material: as well as the dry mites on dry leaves, from which the slides were made, there are a type slide and five paratypes.

REFERENCES CITED

1. **Cecidophyopsis** K.—California Dept. Agric. Bull. 47(4): 273; 1958 (March 13, 1959).
2. **Cecidophyes** Nalepa—Sitzungsber. Akad. Wiss. Wien, math.-nat. Kl. 98: 31; 1889.
3. **Cecidophyes** Nal., genotype designation—California Dept. Agric. Bull. 27: 302; 1938.
4. **Glyptacus** Keifer—California Dept. Agric. Bull. 42: 67; 1953.
5. **Coptophylla** Keifer—California Dept. Agric. Bull. 33: 26; 1944.
6. **Aculus** Keifer—California Bur. Ent. Occas. Paper No. 1: 5; May 8, 1959 (May 12).
7. **Nothopoda** Keifer—California Dept. Agric. Bull. 40: 96; 1951.
8. **Floracarus** Keifer—California Dept. Agric, Bull. 42: 69; 1953.
9. **Nothopodinae** Keifer—California Dept. Agric. Bull. 44: 163; 1955 (1956).
10. **Aceria prostantherae** K.—California Bur. Ent. Occas. Paper No. 1: 17; May 8, 1959 (May 12).

THE COMPARATIVE BIONOMICS OF AMERICAN CRYPTOLESTES[1] (COLEOPTERA-CUCUJIDAE) THAT INFEST STORED GRAIN[2,3]

GUY W. BISHOP[4]

ABSTRACT

C. ferrugineus is the most abundant *Cryptolestes* in collections from northern grain-growing areas. *C. turcicus* is found much more commonly than *C. minutus*, but has frequently been misidentified as the latter. Of the three, *C. ferrugineus* was found least sensitive to low humidities, in both the adult and the larval stages. Egg production and longevity of each species increased sharply with increased relative humidity. When exposed to low temperatures, under both field and laboratory conditions, the tolerances of *ferrugineus* and *turcicus* were similar, but *C. minutus* had a higher mortality than either of the others. Though the three species have similar habits, differences were observed which may be important in survival.

The three species of *Cryptolestes* which infest stored products in America are *Cryptolestes ferrugineus* (Stephans), the rusty grain beetle; *Cryptolestes minutus* (Olivier), the flat grain beetle; and *Cryptolestes turcicus* (Grouville). A fourth species, *Cryptolestes pusilloides* (Steel and Howe), has been recorded from North America on several occasions (Howe 1955; Howe and Lefkovitch 1957). In addition, two specimens collected at Bend, Oregon, in 1930 have been identified as this species by Howe. Howe and Lefkovitch report that this species is confined to the Southern Hemisphere but has reached northern regions

[1]Steel and Howe (1955) considered the species dealt with here as belonging in the genus *Cryptolestes*.

[2]Scientific Paper No. 1808, Washington Agricultural Experiment Station. Work was conducted under Project No. 1127; the research was supported largely from Federal Regional Funds (WM-16) and from substantial grants from the Washington State Department of Agriculture. Accepted for publication February 5, 1959.

[3] Based on a portion of a thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Entomology, State College of Washington. I wish to express my appreciation to Doctors Horace S. Telford, Maurice T. James, and David W. Walker for advice and assistance during this investigation and for criticism of the manuscript.

[4]Present address: University of Idaho Branch Experiment Station, Aberdeen, Idaho.

Table 1.—Number of localities represented by each species in various States.

States	Localities	Species		
		minutus	*turcicus*	*ferrugineus*
British Columbia	1	0	1	0
California	8	3	1	4
Colorado	3	0	0	3
Florida	1	1	0	0
Idaho	7	0	2	6
Iowa	35	2	20	22
Kansas	1	0	1	0
Louisiana	1	1	0	0
Oregon	12	4	1	11
Pennsylvania	1	1	0	0
Texas	1	0	0	1
Utah	1	0	0	1
Washington	17	0	9	11
Total	89	12	35	59

through commerce without becoming established.

Species of *Cryptolestes* are often the most prevalent insects in infestations of stored cereals. According to Howe (1943), Oxley and Howe (1944), and Freeman (1952), they are of particular importance when associated with heating and caking of bulk grain. Farrar and Flint (1942) report species of *Cryptolestes* to be among the most important pests of shelled corn in Illinois.

Information on the bionomics of the three species has come largely from Rilett (1949) on *ferrugineus* and Davies (1949) on *minutus*. Payne (1946) briefly described the life cycle of *minutus*. Williams (1954a and 1954b) contributed information on the bionomics of *minutus* with special reference to the effects of nutrition and exposure to low temperatures. Davies (1949) has summarized the literature on the products found infested by these species.

DISTRIBUTION IN NORTH AMERICA

The distributional records of the specimens examined during this study are summarized in table 1. Although these specimens do not represent a sufficiently broad area to allow definite conclusions, they indicate that *ferrugineus* is most common, being represented in 59 of the 89 localities from which specimens were available. *C. turcicus* was recorded from nearly three times as many localities as *minutus*; however, a majority of the records were made in States with low winter temperatures. The rarity of American references to *turcicus*, even though it is probably more common than *minutus* in the northern grain growing areas, is undoubtedly due to its being confused with *minutus*, or in some cases, with *ferrugineus*.

In identifications of *Cryptolestes* spp. collected on ships of American origin in British ports, Howe and Lefkovitch (1957) recorded 116 occurrences of *ferrugineus*, 23 of *turcicus*, and 22 of *minutus*. Of 30 collections of *turcicus* found in produce from various parts of the world by Howe (1955), 14 were from North America, indicating that this species is relatively more abundant on this continent than in other parts of the world.

TEMPERATURE AND MOISTURE

General Methods and Equipment.—The same laboratory cultures of the three species were used throughout the investigation. Original specimens for the cultures of *ferrugineus* and *turcicus* were obtained from a grain elevator near Pullman, Washington, and those for *minutus* at Vale, Oregon. Stock cultures were reared on soft, white, cracked wheat in quart fruit jars covered with cloth lids. The rearing room was maintained at about 80° F. with approximately 80 percent RH.

Relative humidities of 40 to 90 percent were obtained by using solutions of potassium hydroxide, and 95 percent RH was obtained with a saturated salt solution.

Temperature cabinets with both heating and cooling units were used for temperature control. Temperatures were not observed to fluctuate more than 2° F. during the experiments.

The sexes in *minutus* and *turcicus* are distinct, but in *ferrugineus* they may be confused in some cases. When sexing was necessary in the latter, the adults were placed in a petri dish resting on cracked ice. Females inactivated in this manner exsert the genitalia when a slight pressure is applied to the ventral surface of the abdomen. This method is discussed by Rilett (1949).

Adults and larvae were removed from cultures with various sized screens to concentrate them in the medium. The medium was then spread out on a piece of toweling, and by gently shaking the toweling, most of the medium could be removed. The adults and larvae which remained clinging to the toweling were brushed onto a smooth surface and picked up with an aspirator.

Table 2.—Effect of temperature and relative humidity on reproduction and longevity of *Cryptolestes* spp., Pullman, Washington, 1955.

Relative humidity %	Average offspring		Average longevity			
			Male		Female	
	70° F.	90° F.	70° F.	90° F.	70° F.	90° F.
			ferrugineus			
40	1.4	2.2	130	78	164	93
50	1.4	4.9	162	72	190	134
60	2.0	7.0	176	74	208	118
70	2.5	17.8	174	106	226	114
90	37.3	33.4	260	133	284	179
Average.....			180.4	92.6	214.4	133.6
			minutus			
40	1.6	0.0	102	36	92	46
50	4.5	4.4	106	54	108	46
60	13.2	6.6	118	60	142	68
70	16.7	11.7	148	78	134	92
90	85.1	96.8	242	98	244	138
Average.....			143.5	65.2	144.0	78.0
			turcicus			
40	1.3	0.2	84	40	74	42
50	5.4	1.9	118	42	108	42
60	10.0	3.8	146	46	102	60
70	21.8	8.6	146	76	138	78
90	131.0	45.5	196	72	188	73
Average.....			138.0	55.2	122.0	59.0

Effect on Egg Production.—Two experiments were conducted to determine the effects of temperature and relative humidity on egg production. The first was set up at relative humidities of 40, 50, 60, 70, and 90 percent at 70° and 90° F.[5] One pair of beetles was placed in each of 10 small cages for each relative humidity and supplied with about ½-gram of food consisting of equal parts of whole wheat flour and wheat germ. All eggs, larvae, and pupae were removed and counted each 20 days and the adults were returned to the cage with fresh food. Dead males were replaced at each count. Egg production was therefore based on total offspring. Although a stereoscopic microscope was used in making the counts, and dead larvae and unhatched eggs were recorded, the counts are no doubt somewhat lower than the actual egg production.

The second experiment was carried out at 90° F., and at relative humidities of 40 to 90 percent with 10 percent intervals. Each pair of adults was placed in a cage constructed from the bottom portion of a shell vial. Food consisted of a few flakes of wheat germ. Eggs were counted and removed every 3 to 4 days and new flakes of wheat germ were added. This experiment was conducted to supplement the data of the first experiment, and to make observations on oviposition rate as related to periods of the adult life span.

The results of the first experiment are in table 2. These data show that with each species, egg production increased with increasing relative humidities. This was most marked with an increase in relative humidity from 70 to 90 percent. *C. ferrugineus* appears less sensitive to a relative humidity of 40 percent at 90° F. At 70° there is little difference between the three species at this low humidity. Grouping the humidities makes it clear that the total egg production of *turcicus* was much greater at 70°, the egg production of *minutus* was nearly equal at both temperatures, and that of *ferrugineus* was slightly higher at 90°. On an egg-per-day basis, the production rate of both *minutus* and *ferrugineus* about doubled at 90°, but the rate of *turcicus* was still about one-third less than at 70°.

The second experiment, summarized in table 3, clearly substantiates that egg production increases sharply with an increase of relative humidity in the range of 40 to 90 percent. The results are also similar in that *ferrugineus* was again less sensitive to a relative humidity of 40 percent than *minutus* or *turcicus*, and the tem-

[5]The series of 80 percent RH was lost because of contamination of the humidifying solution.

Table 3.—Average egg production of *Cryptolestes* spp. at various relative humidities during three periods of the life span, 90° F., Pullman, Washington, 1956.

Relative humidity %	Periods of life span			Average Total eggs	Longevity of female (days)
	First one-third	Second one-third	Final one-third		
			ferrugineus		
40	0.4	3.7	0.5	4.6	36.6
50	2.9	4.6	0.4	7.9	56.7
60	7.1	12.5	3.9	23.5	68.9
70	11.1	17.1	6.3	34.5	77.6
80	16.4	10.9	4.0	31.3	72.2
90	14.7	17.8	13.0	45.5	72.0
Total	52.6	66.6	26.7	147.3	
			minutus		
40	0.3	0.5	0.0	0.8	17.5
50	4.7	8.6	6.8	20.1	76.0
60	14.7	18.3	9.0	42.0	84.1
70	18.4	19.6	12.9	50.9	75.9
80	45.7	25.4	14.4	85.5	79.1
90	72.1	41.5	20.5	134.1	86.5
Total	155.9	113.9	63.6	334.4	
			turcicus		
40	0	0	0	0	16.1
50	0.4	0.1	0	0.5	42.0
60	1.5	3.5	0.2	5.2	51.7
70	2.9	2.7	1.0	6.6	72.5
80	3.7	5.9	1.1	10.7	51.5
90	26.9	21.0	5.7	53.6	65.6
Total	35.4	33.2	8.0	76.6	

perature of 90° appears to be less favorable to *turcicus* than to the other two species. The somewhat higher egg production of all species when compared with the same temperature in the first experiment probably resulted from a more accurate measure of egg production as well as the higher protein content of the food used.

When the adult stadia of the three species are divided into three periods as in table 3, it is apparent that all produce fewer eggs late in life. Only 15 of the 144 females involved deposited as many as one-third of their eggs during the final one-third of their life. There was considerable variation among individuals during the first two periods, but there was a tendency, particularly in *minutus*, for increased oviposition during the first period in direct proportion to increased relative humidity.

Effect on Longevity.—The longevity of both sexes of the three species was increased sharply at 70° F. when compared with 90° (table 2). This effect was most pronounced on *turcicus*, again suggesting that the optimum temperature for this species is below 90°. Although there was an increased longevity with increased relative humidity, the effect was not nearly as pronounced as that of temperature. At both temperatures and all humidities the longevity of *minutus* and *turcicus* was consistently shorter than that of *ferrugineus*, but the difference was greatest at the lower humidities. The female of *ferrugineus* was distinctly longer-lived than the male, but there was no consistent difference between the sexes in the other two species. The shorter longevities in the second experiment may have been caused by the frequent handling and removal of the adults from their environment.

Rilett (1949), working with *ferrugineus*, obtained a mortality of 97 percent after 330 days when a series of adults were isolated singly with food at 90° F. and 75 percent RH. This finding agrees well with the longevity observed for this species under similar conditions in the first experiment of the present study. The maximum longevity of 504 days reported by Davies (1949) for *minutus* is somewhat greater than that observed for this species in the present study.

Effect on Duration of Stages.—To determine the effect of relative humidity on the duration of the stages, the life cycles of the three species were observed at relative humidities of 40 through 90 percent with 10 percent intervals, at a temperature of 90° F. One egg, less than 8 hours old, was placed in each of 15 cages for each

Table 4.—Average duration of stages of *Cryptolestes* spp. at various humidities (in days).

Species and humidity	Larval stadia						Egg to adult
	Egg	First	Second	Third	Fourth	Pupa	
				ferrugineus			
40	3.9 (14)[a]	———	———	———	———	———	———
50	4.0 (13)	———	———	———	———	———	———
60	3.7 (15)	5.1 (10)	3.6 (9)	4.0 (9)	6.4 (9)	4.3 (9)	27.0
70	3.8 (13)	4.3 (11)	3.9 (9)	7.5 (9)	7.5 (9)	4.4 (9)	27.5
80	3.6 (13)	3.7 (13)	2.3 (13)	3.4 (13)	6.6 (13)	4.5 (13)	24.0
90	3.9 (15)	3.3 (15)	2.4 (15)	2.7 (15)	6.6 (15)	4.0 (15)	23.0
95	4.0	2.5	1.7	2.0	———	———	———
Average[b]	3.8	4.1	3.0	3.5	6.8	4.3	25..7
				minutus			
40	6.6 (6)	———	———	———	———	———	———
50	4.1 (14)	———	———	———	———	———	———
60	4.0 (14)	———	———	———	———	———	———
70	3.5 (15)	6.6 (7)	3.5 (7)	5.8 (6)	6.2 (6)	4.5 (6)	29.2
80	3.5 (13)	5.5 (9)	4.4 (9)	4.1 (9)	6.2 (9)	4.2 (9)	28.7
90	3.5 (15)	4.0 (13)	3.6 (11)	3.3 (11)	7.0 (11)	4.4 (11)	27.3
95	3.6	2.2	1.2	1.7	———	———	———
Average	4 2	5.4	3.8	4.4	6.5	4.4	28.4
				turcicus			
40	5.2 (6)	———	———	———	———	———	———
50	3.5 (14)	———	———	———	———	———	———
60	3.0 (13)	———	———	———	———	———	———
70	3.0 (13)	7.0 (1)	———	———	———	———	———
80	3.1 (15)	6.0 (5)	5.5 (4)	7.5 (3)	8.5 (3)	4.0 (3)	35.0
90	3.5 (15)	4.2 (9)	4.3 (8)	3.8 (8)	7.8 (8)	4.4 (8)	28.7
95	3.0	3.0	1.7	3.0	———	———	———
Average	3.5	5.7	4.9	5.6	8.1	4.2	31.8

[a]Number in parentheses is the number of individuals completing the stage concerned.
[b]Average of all humidities except 95 percent.

species at each humidity. The food supply consisted of one-half kernel of wheat which had been split longitudinally so that a portion of the germ remained on each piece. Observations were made at 24-hour intervals. Larvae of *minutus* and *turcicus* were removed from their cocoons to observe the pupae. The presence of a cast skin in a cage was used for the determination of an instar.

Increased relative humidities decreased the mortality of each species (table 4). Only 10 of the 93 larvae which survived the first stadium failed to reach adulthood, showing that the greatest effect of relative humidity is on the first instar. A high mortality of the eggs of *minutus* and *turcicus* occurred at 40 percent RH but the eggs of *ferrugineus* were not affected. Similarly, the first instar of *ferrugineus* was less affected by the lower humidities than that of *minutus* or *turcicus*. The high mortality of the latter species, even at the higher humidities, may have resulted because the temperature was above the optimum for development as was indicated previously by the egg production data.

With an increase in relative humidity there was a decrease in the total length of the developmental periods of the species, largely of the first three instars. The duration of the egg stage of *minutus* and *turcicus* was lengthened at 40 percent. No pronounced effect of relative humidity on the duration of the fourth larval or pupal stadium was evident in any of the species.

The average time from egg deposition to adulthood was shortest in *ferrugineus* and longest in *turcicus*. The relative lengths of the stadia of all three species were similar. The second was shortest, followed by the third, first, and fourth, respectively.

Observations were seriously limited at 95 percent RH because of mold growth on the food. It was not possible to determine time of death of larvae or duration of stadia beyond the third. However, the third instars that were observed appeared about normal in size, indicating that the short durations of the first three stadia were not due to supernumerary moults. Apparently the food supply was depleted by the molds when the larvae were in the third stadium, because the adults which ultimately emerged were extremely dwarfed. It is possible that in natural infestations where the larvae could move to a new food source, the life cycle would be considerably shortened under conditions of high moisture.

These results generally agree with those of

Table 5.—Number of live adults of *Cryptolestes* spp. after exposure to 40° F. for various periods, Pullman, Washington, 1956.

Replicate	Days exposure						
	2	12	24	33	42	56	66
			ferrugineus				
1	49	35	24	20	15	9	5
2	49	30	21	21	18	11	5
3	50	38	25	24	19	10	6
4	49	36	29	22	16	6	4
Average.....	49.2	34.7	24.7	21.7	17.0	9.0	5.0
			minutus				
1	48	38	0	—	—	—	—
2	47	8	0	—	—	—	—
3	46	15	0	—	—	—	—
4	47	15	0	—	—	—	—
Average.....	47.0	18.7					
			turcicus				
1	50	48	42	35	29	19	5
2	50	48	46	41	33	17	6
3	49	47	42	26	20	12	7
4	48	46	45	36	26	18	8
Average.....	49.2	47.2	43.7	34.5	27.0	16.5	6.5

Davies (1949). He found that relative humidity changes had little effect on the egg and pupa of *minutus*, but the first larval instar, and to a lesser extent the others, succumbed to dry conditions. He also found that low humidities retarded development of the larval stages but that temperature was more important in determining the length of the life cycle. Rilett (1949) reports that an increase in relative humidity from 50 to 75 percent accelerated the development of *ferrugineus*. The present study shows that the life cycle of *ferrugineus* is shorter than that of *minutus* under similar conditions of temperature and humidity. This result agrees with the observations of Davies (1949) and of Rilett (1949).

Effect of Low Temperatures.—Extreme differences in susceptibility to low temperatures were indicated when adults of the three species were caged and placed in bins of wheat being experimentally cooled during winter months by forced circulation of outside air. After several months' exposure, the mortality of *minutus* was 100 percent while that of *turcicus* and *ferrugineus* was 8 and 12 percent, respectively.

Three laboratory experiments were conducted to obtain further information. In the first experiment, at 40° F., only adults were included. Both adults and fourth-stage larvae were used in the other two experiments run at 26° and 32° F. In each case the insects were put in small jars containing whole-kernel wheat which had a moisture content of about 16 percent. In the first experiment the adults were returned to the same environment after each count so that the same insects were used throughout the experiment. In the other two experiments a different group of insects was used for each time interval.

The results of these experiments show that *minutus* is much more sensitive to low temperatures than either *turcicus or ferrugineus* (tables 5, 6, and 7). *C. ferrugineus* was more susceptible than *turcicus* during the first part of the exposure periods but just as tolerant to prolonged exposures. The fourth larval instar of *minutus* appears to be somewhat less susceptible to low temperatures than the adult, but *ferrugineus* and *turcicus* adults were much less susceptible.

Williams (1954a), in comparing the tolerance of the various stages, found the egg of *minutus* most susceptible to 36° F., followed in order by the first, second, and third larval instars. The fourth instar and the pupa were more resistant than the adult. The adult male was more susceptible than the female. Neither variation of atmospheric humidity nor previous starvation of the adults affected mortality. Soloman and Adamson (1955) found *ferrugineus* to be more cold-hardy than *turcicus* or *minulus*.

HABITS

Since most of the experimental work on temperature and humidity was conducted with caged pairs of adults or individually caged larvae, ample opportunity was available for comparing

the habits of the three species. As would be expected, there are many similarities in their habits, but differences which may be of importance to their survival do exist.

Mating.—A rather complete account of the process of mating in *ferrugineus* has been given by Rilett (1949). Little variation from this account has been observed in the other two species.

C. ferrugineus remains in copulation longer than *minutus* or *turcicus* and is less sensitive to disturbances during this time. Transferring copulating pairs of *ferrugineus* from one container to another often did not cause separation, but the sensitivity of the other two species was so great that they were observed to separate upon sudden exposure to light.

Davies (1949) has shown that the egg production of the female of *minutus* is increased by the constant presence of the male even though mating has occurred. Limited observations indicate that the same condition exists with *minutus* and *turcicus*. Isolated pairs of all three species were observed in copulation at various times during their oviposition periods, but mating was observed much more frequently in *ferrugineus*.

Oviposition.—Oviposition in all three species commences within 1 to 2 days after mating. After many observations, it was concluded that none of the species oviposits in the absence of mating. Eggs are normally inserted into cracks or crevices if such locations are available, but may be deposited loosely in the food material. When whole-kernel wheat is the food, many eggs are inserted into minute cracks in the germ area. When adults are numerous it is not uncommon to find several eggs in most of the kernels having such flaws. The newly-deposited egg is very flexible and can be inserted into the germ area through cracks which are apparently smaller than the diameter of the egg. In ground wheat, *minutus* often deposits eggs in the webbing formed by the fourth stage larvae.

Under cage conditions, eggs may be deposited singly or in groups of 10 or more in a particular location. It was not uncommon for the female to deposit several eggs one day, and none thereafter for several days. The presence of feces within small cages was found to inhibit egg production even though fresh food was available.

Feeding.—As shown by Williams (1954a) with *minutus*, the species distinctly prefer the germ of wheat as food, and probably the germ of other cereals as well. The endosperm may be attacked but usually not extensively until after the germ has been consumed. The larvae may form tunnels during feeding or simply hollow out a section of the kernels. It is usual for a large portion of the kernels which had original breaks in their covering to be completely hollowed out when a culture is kept under favorable conditions for several months.

The adults and larvae also feed on particles that adhere to the webbing produced by the fourth stage larvae of *minutus*. This webbing appears to be a preferred place for larval development, particularly the early instars. The larvae of *turcicus* were not observed to produce the large amounts of webbing which *minutus* does.

Table 6.—Number of live adults and larvae of *Cryptolestes* spp. after exposure to 32° F. for various periods, Pullman, Washington, 1956.

Stage	Hours exposure						
	24	39	47	55	120	144	192
				ferrugineus			
Adult	49	48	48	40	39	41	26
Larval	48	35	33	30	22	0	2
				minutus			
Adult	37	15	3	1	0	0	0
Larval	50	41	30	23	8	2	0
				turcicus			
Adult	50	50	47	47	46	39	35
Larval	50	50	46	38	27	17	6

Cocoon Formation.—Cocoons are formed by the prepupal phase of the fourth instar in *minutus* and *turcicus*. In countless observations no cocoon formation was observed by *ferrugineus*. However, a small amount of silk was produced by the larvae of this species on several occasions, showing that the silk glands are functional. *C. minutus* did not pupate without cocoon formation. According to Williams (1954a), this species sometimes pupates without a cocoon when conditions are unfavorable for development. In the present study, *turcicus* pupated without cocoon formation on several occasions under favorable developmental conditions.

Pupation.—When whole grain is the food, pupation usually occurs in the hollowed-out cavity within a kernel. The cocoons of *minutus* and *turcicus* fill a large part of the cavity. When the larva has fed in the germ area, it forms a seal over the break in the seed coat through which entrance was gained. The burrow of *ferrugineus* is plugged with frass and the naked pupa is formed behind this protection. When pupation in any of the species occurs outside of the kernel, a protected place such as the space between kernels is usually chosen. Under laboratory conditions in meal cultures, clusters of cocoons of *minutus* are often found loosely tied together with webbing.

Activeness of Adults.—The adults of the three species differ considerably in activity. Under similar conditions *ferrugineus* moves much more rapidly than the other two and can nearly always

be distinguished by the uneven pattern of its movements. *C. turcicus* is about intermediate in its rate of movement, and it, as well as *minutus*, moves much more smoothly than *ferrugineus*.

When the adults are concentrated in small amounts of their food, *minutus* is much more likely to remain in the food mass than either *turcicus* or *ferrugineus*. In separating adults from media for various tests, it was necessary to remove many individuals of *minutus* from food particles by hand.

Flight.—Each of the three species was observed to take flight on several occasions. Although no detailed studies were conducted, laboratory observations show that flight takes place at temperatures above 80° when the adults are separated from their food. At temperatures near 100° they showed a tendency to cluster on top of their food and attempt to take flight. Observed flights usually commenced in a vertical spiral, but were ultimately in the direction of a light source. Under the same conditions the tendency to take flight appears to be stronger in *ferrugineus* and *minutus* than in *turcicus*.

Cotton et al. (1953) collected species of *Cryptolestes* both in traps installed in ventilators of steel bins and in rotary traps 3 and 6 feet above the ground. The rotary traps were near grain storage facilities. Catches were made from July to September. Schwitzgebel and Walkden (1944) collected *minutus* in rotary traps and sticky boards in the vicinity of storage facilities. Adults were caught also in ventilator traps as they were attempting to enter storage facilities. Barnes and Kaloostian (1940) collected *Cryptolestes* spp. in a rotary trap in a raisin storage yard. Highest numbers were recorded during hot weather, and flights were particularly common during late afternoon and evening. Specimens collected by Barnes and Kaloostian during their study were examined by this writer and found to be *ferrugineus*.

Cannibalism.—Rilett (1949) reports that *ferrugineus* is cannibalistic, with the immobile prepupal and pupal stages as the usual victims. Payne (1946) found no indication of cannibalism in *minutus*, but Williams (1954a) reports that cannibalism may occur in this species when the diet is unfavorable. In the present study, an adult female of *ferrugineus* was observed to consume a series of eggs. The female, which had been starved, was confined in a small container with the eggs. After moving around the cage rapidly for several minutes, pausing occasionally to examine an egg, she consumed first one, then the others in rapid succession. Eggs offered to adults of *minutus* and *turcicus* under similar circumstances were not taken. Larval remains were found in cultures of all three species, but such findings show only that these species can be scavengers and do not necessarily indicate a predacious activity.

Kernel Damage.—Several workers (Davies 1949, Rilett 1949, Fraenkel and Blewett 1943, and Williams 1954a) have shown that *Cryptolestes* can not infest perfectly sound kernels of grain.

With the three species studied, the percentage of infested kernels was never higher than the percentage of kernels with original flaws in their seed coats. This was true even though the samples were exposed for long periods under optimum conditions. However, kernels subjected to high moisture, and with the germ covering ruptured by partial germination, are subject to infestation.

Table 7.—Number of live adults and larvae of *Cryptolestes* spp. after exposure to 25° F. for various periods, Pullman, Washington, 1956.

Stage	Hours exposure			
	8	16	24	36
		ferrugineus		
Adult	44	42	40	44
Larval	45	39	33	26
		minutus		
Adult	44	0	0	0
Larval	20	4	0	0
		turcicus		
Adult	49	43	45	44
Larval	44	40	38	34

To estimate the percentage of kernels normally having flaws, 10 samples of soft winter wheat were taken from elevators in the vicinity of Pullman, Washington. Flaws in these samples ranged from 30 to 60 percent. These consisted mostly of slight breaks in the germ covering, but kernels otherwise cracked or broken were also encountered.

Two infestations of wheat stored near Pullman, which apparently involved only *ferrugineus*, were observed. Both infestations appeared to have originated in wheat dampened from a roof leak. The grain was caked and sprouting to a depth of 3 to 4 inches. Below this layer the grain was very moist but not sprouting, and heavily infested with all stages. Freeman (1952) discussed numerous outbreaks of *Cryptolestes* spp. as the dominant or sole pest in grain stored in the United Kingdom. His work pointed out that these insects, often considered as secondary pests incapable of attacking whole grain, may sometimes cause initial grain heating. McLaine (1943) has reported on similar infestations of *Cryptolestes* in Canada.

In consideration of the published information

as well as personal observations, the infrequency of infestations involving only *Cryptolestes* must be attributed to the general occurrence of other stored-products pests in storage facilities rather than to the inability of *Cryptolestes* to develop independently of the other pests.

Hybridization.—To determine if hybridization among the three species was possible under laboratory conditions, pairs were enclosed in small rearing vials in the six possible combinations. A series of 10 vials was used for each combination. The adults were reared from individually caged larvae to insure virgin material. No matings were observed during the 6 weeks' duration of the test, and no eggs were deposited. When males and females of the same species were united after the test, mating occurred within a few minutes.

Observations made on the pairs during the attempted crosses revealed that the male frequently made the customary advances and showed signs of excitement, but the advances did not elicit the necessary responses from the female.

REFERENCES CITED

Barnes, D. F., and **G. H. Kaloostian.** 1940. Flight habits and seasonal abundance of dried fruit insects. Jour. Econ. Ent. 33: 115–9.

Cotton, R. T., H. H. Walkden, G. D. White, and **D. A. Wilbur.** 1953. Causes of outbreaks of stored-grain insects. Kansas Agric. Expt. Sta. Bull. 359. 36 pp. (North Central Regional Publication 35.)

Davies, R. G. 1949. The biology of *Laemophloeus minutus* Oliv. (Col., Cucujidae). Bull. Ent. Res. 40: 63–82.

Farrar, M. D., and **W. P. Flint.** 1942. Control of insects in fourteen thousand grain bins. Jour. Econ. Ent. 35: 615–9.

Fraenkel, G., and **M. Blewett.** 1943. The natural food and food requirements of several species of stored products insects. Trans. Roy. Ent. Soc. London 93: 457–90.

Freeman, J. A. 1952. *Laemophloeus* spp. as major pests of stored grain. Plant Pathol. 1(3): 69–76.

Howe, R. W. 1943. An investigation of the changes in a bin of stored wheat infested by insects. Bull. Ent. Res. 34: 145–58.

1955. *Laemophloeus turcicus* (Grouv.) (Col. Cucujidae) in the U. S. A. Ent. Mon. Mag. 91: 63.

Howe, R. W., and **L. P. Lefkovitch.** 1957. The distribution of storage species of *Cryptolestes* (Col. Cucujidae). Bull. Ent. Res. 48: 795–809.

McLaine, L. S. 1943. War activities of the Federal Divisions of Entomology and Plant Protection since 1939. 73rd Rept. Ent. Soc. Ontario: 7–16.

Oxley, T. A., and **R. W. Howe.** 1944. Factors influencing the course of an insect infestation in bulk wheat. Ann. Appl. Biol. 31: 76–80.

Payne, N. E. 1946. Life history and habits of the flat grain beetle, *Laemophloeus minutus* Oliv. Jour. New York Ent. Soc. 54: 9–12.

Rilett, R. O. 1949. The biology of *Laemophloeus ferrugineus* (Steph.). Canadian Jour. Res. (D) 27: 112–48.

Schwitzgebel, R. B., and **H. H. Walkden.** 1944. Summer infestation of farm stored grain by migrating insects. Jour. Econ. Ent. 37: 21–24.

Soloman, M. E., and **B. E. Adamson.** 1955. The powers of survival of storage and domestic pests under winter conditions in Britain. Bull. Ent. Res. 46: 311–55.

Steel, W. O., and **R. W. Howe.** 1955. A new species of *Cryptolestes* (Coleoptera: Cucujidae) associated with stored products in Africa. Proc. Roy. Ent. Soc. London (B) 24: 107–9.

Williams, G. C. 1954a. Observations on the life history of *Laemophloeus minutus* (01.) (Col. Cucujidae) when bred on various stored cereals and cereal products. Bull. Ent. Res. 45(2): 341–50.

1954b. Observations on the effect of exposure to a low temperature on *Laemophloeus minutus* (01.) (Col. Cucujidae). Ibid. 351–9.

THE FURCOPLEURAL MUSCLES OF LEPIDOPTERA[1]

L. E. CHADWICK

Department of Entomology, University of Illinois, Urbana

ABSTRACT

Despite reports to the contrary, furcopleural muscles are characteristically present in the pterothorax of Lepidoptera. This paper outlines the main distribution of such muscles among insects, and discusses general features of their function and structural variation. Attention is called to peculiarities in the arrangement of these muscles in Lepidoptera.

The furcopleural muscles of Lepidoptera are much like those of other insects, although there has been some confusion about them. In particular, Weber (1924, 1928), despite an earlier description for *Sphinx* (Berlese 1909) and his own work with *Hepialus*, failed to find these muscles in the winged segments of *Papilio machaon* L.; and cited their supposed absence there in support of theories in regard to the structure and evolution of the neuropteroid thorax. He summarized (1928, p. 214), "Thus in Lepidoptera a skeletal union of the furca with the epimeron takes the place of the [usual] muscular connection of the furca with the pleural ridge." Now, this statement is at best only partially true, as witnessed, for example, by some of Weber's own dissections; but Weber's generalization has recently been given wider circulation by Pringle (1957, p. 32) in his work on insect flight. Since Pringle's book deservedly enjoys the careful attention of all

[1]Accepted for publication March 20, 1959.

students of animal function, it is especially important not to leave unquestioned any morphological misinterpretations that might be drawn from it.

There can be no doubt that, as Weber remarked, a fusion of furcal and epimeral parts is highly developed in the Lepidoptera, apparently as a result of sclerotization that has advanced gradually along the course of former furcoepimeral or furcopostcoxal muscles or ligaments. Developments of this sort in some other insects were pointed out by Chadwick (1957, p. 15); and muscles or ligaments of this nature occur in comparable positions in certain more primitive neuropteroids also. They are represented, for instance, in Megaloptera (Czihak 1953, in *Sialis;* Kelsey 1957, in *Corydalus*), where they may be transformed in varying degrees, depending on the species, to endoskeletal braces. Formations of this kind were not seen by Weber (1924, 1928) in his preparations of *Sialis*, although they probably were present, to judge by Czihak's later report and my own examination of two North American species of this genus. In any case, they can in no sense be regarded as replacements for the furcopleural muscles, with which they often occur concurrently. Moreover, furcopleural muscles, together with furcoepimeral bridges, have now been reported for the pterothorax of *P. thaiwanus* Rothschild by Maki (1938) and in four North American species of *Papilio* by Chadwick (1939), while both authors invariably found such furcopleural muscles and furcoepimeral bridges present together in assorted species from other families throughout the order. Thus, absence of the furcopleural muscles from *P. machaon*, even if corroborated, could not be considered a general characteristic of the order, nor even of the small section of it that includes the swallowtailed butterflies.

Apart from the advanced condition of the furcoepimeral fusion, with which Weber was impressed, and which is seen to be quite characteristic of the Lepidoptera, there are in the sternopleural unions of these insects at least two other distinctive features to which attention should be given. These occur in the furcopleural muscles themselves, and may best be pointed out in connection with a more general consideration of the function and distribution of the furcopleural muscles in insects.

In the moths and butterflies, furcopleural muscles are represented in all three thoracic segments, although extensive ingrowths from the integument have always replaced the originally contractile connection in the prothorax. Here, the now appressed portions of the sternal arm and pleural ridge are joined to one another firmly to form an endoskeletal bridge, a modification of structure that was apparently made early in the neuropteroid line or perhaps even before the separation of ancestral neuropteroids from other insects. Whether one chooses to interpret the development in different groups as due to common inheritance or to convergence, the fact is that it has been reported for all species of Megaloptera, Neuroptera, Mecoptera, Coleoptera, Trichoptera, Lepidoptera and Diptera on which suitable studies have been made (references in Chadwick 1959); so that it seems safe to say that only the exceptional neuropteroid insect lacks such a union in the prothorax. Concomitantly, one concludes that developments of this sort can not be related solely to the forces imposed on a thoracic segment by the demands of wing motion. Among the orders considered neuropteroid, the fusion may be absent in certain parasitic species of otherwise highly modified structure, and in those larval Holometabola that have diverged widely from the original hexapod organization; but granted such exceptions the fusion may be thought of as a typical neuropteroid feature, even though a similar fusion is found in a number of nonneuropteroid groups. There are also, as it happens, several nonneuropteroid orders in which a persisting contractile muscle or a ligamentous strap still connects the prosternal arm or its equivalent with the prothoracic pleural ridge.

In the winged segments of all neuropteroid orders, the sternal arm is joined to the corresponding pleural ridge by a muscle; and, as mentioned above, the Lepidoptera are typical in this respect. However, the tendency for replacement of the muscular union by sclerotization may often be detected in these segments also; only here it seems never to have progressed, as it has in several nonneuropteroid insects, to complete fusion of the furcal arm with the pleural ridge. Thus, though some muscular tissue is always present in the pterothoracic furcopleural unions of lepidopterous species, the insects display considerable specific differences in the ratio of muscular to nonmuscular elements in the entire complex, much of the distance between the primitive sites of muscle attachment being occupied now by an extension of one or the other skeletal part. Such variation, which is quite uncommon in other insect orders, so far as is known, is the first of the noteworthy features of the furcopleural muscles in the Lepidoptera to which we would call attention; and it even seems possible that such variations might be useful in gauging the relationships of some of the species concerned.

In another respect, the furcopleural muscles of the lepidopteran thorax appear to be unique. Here, in each of the winged segments, the muscle is of roughly conical form, originating by a broad base and inserted by a relatively thin sclerotized rod or tendon. This shape of furcopleural muscle is likewise seen in some other orders; but, unlike them, the Lepidoptera have a peculiarly contrasting arrangement of these muscles in the two winged segments. In this

order, and apparently in this order only, the broad origin is on the pleural ridge in the mesothorax and on the sternal arm in the metathorax.

Before we proceed to consider these lepidopteran peculiarities further, a statement as to the functions of sternopleural muscles in general will be helpful. We may suppose that, in primitive insects or their ancestors, a muscle in this position served primarily to move the connected parts relative to one another. With increasing overall sclerotization, and especially with the coordination of sternum and pleuron to form a firm base upon which to move the appendage, the motor function of a sternopleural muscle was reduced. However, such a connection still retained much usefulness as a brace that would hinder excessive relative displacement of the attachment sites. The subsequent fate of the furcopleural muscles may be followed in many lines of descent. The contractile tissue has often been replaced, first by ligaments that passively oppose only tension exerted along their main axis, and later by sclerotized inward extensions from the skeletal attachment that can withstand compressive forces in various directions as well. Numerous stages of such a process are preserved in different insects and in the different levels of modification reached in their several thoracic segments.

Although it seems assured, as indicated above, that the underlying cause of such developments cannot lie wholly in the needs of flight, it is certain that the advent of flight must have put special stresses on these internal bracing systems, for it is essential that the powerful dorsoventral and longitudinal flight muscles be prevented from wasting energy merely in bowing outward the upper margin of the pleuron, which carries the pleural fulcrum of the wing. The pleural wing processes would undoubtedly move in such a manner were it not for the restraining influence of the junction between the pleural ridge and the median region of the sternum.

A more subtle contribution of a furcopleural muscle to flight has been described by Boettiger and Furshpan (1950, 1952; reviewed by Pringle 1957), who have found that the extent of the excursion of the wings in flies is regulated by a "snap mechanism." According to their observations, tension in the main wing-driving muscles of flies builds up rapidly when the muscles are activated, but without appreciable shortening of the muscles until the tension is reached at which the catch of the "snap mechanism" is sprung. The wing then sweeps suddenly through the full extent of its arc, the muscles relax immediately when thus relieved of tension, and much of the work that would be brought about by internal shortening is avoided. The furcopleural muscles enter the picture because the critical tension at which wing movement occurs depends upon the degree of loading of the catch, and this in turn is regulated by the pull developed by the furcopleural muscles. Thus, the mechanism for the movement of the wing, and the amplitude of movement particularly, may be governed, in these species, by the relatively slow-acting furcopleural muscles. Obviously, a mechanism of exactly this sort cannot be at work in those insects in which the pterothoracic furca and pleural ridge are firmly fused; although there are other ways in which a comparable result might be achieved. There are indeed indications that a "snap mechanism" of some kind may be more generally involved in insect flight than has hitherto been realized; but, on the basis of present knowledge, it seems likely that many species may produce and control their wing movements in quite a different manner.

In the Lepidoptera, it is the static bracing function of the furcopleural union that has clearly become predominant. Though the muscular portion of the complex still exists, in most instances it is small, in some it is of degenerate appearance, and in others the connection between furca and pleuron is almost completely sclerotized. We must remember too that in this order, a firm thoracic structure, so basic to proper operation of the wings, is assured by three further developments. All of these have been emphasized rightfully by Weber (1924, 1928), though, as we have seen, some of his explanations of their phylogeny are open to doubt. One of these developments is the strengthening and extension of the lateral body wall by the incorporation in it of the coxal segment of the leg. A second change, which may be followed through the series of neuropteroid orders, is the growth of the furcoepimeral junction, to which we have referred above. A third factor in Lepidoptera that ensures the fixed position of the pleuron is a fusion, probably earlier in origin, between the more anterior sternal and the episternal elements. Of these four developments, all of which seem traceable to a similar driving force, the fusion between furca and pleural ridge is obviously the most recent in occurrence, since it still lacks morphological completion here, as it does in many other orders.

The considerations we have outlined hold for both the pterothoracic segments of Lepidoptera, but they do not explain why the origin and insertion of the furcopleural muscle should be reversed in them. No doubt this curious inversion has, or had, some functional basis; but, since it is not found in the Trichoptera, one can only surmise that it may be connected in some way with the customary reduction, in the Lepidoptera, of the metathoracic wings, a development that apparently first became appreciable here in the line that led to the Jugatae. Against the attempt to account for the inversion in such a way is the fact that no such reversal seems to occur in the Hymenoptera and Diptera,

both of them orders which show an even greater relative reduction of the hindwings than the Lepidoptera; so that, in the absence of alternative suggestions, the reason for the difference in the two segments of the Lepidoptera is at present wholly obscure.

REFERENCES CITED

Berlese, A. 1909. Gli insetti. Milano: Soc. Edit. Libraria. Vol. 1, xii+1064 pp., 10 pls.

Boettiger, E. G., and **E. Furshpan.** 1950. Observations on the flight motor of Diptera. Biol. Bull. 99: 346–7.

1952. The mechanism of flight movements in Diptera. Biol. Bull. 102: 200–211.

Chadwick, L. E. 1939. Comparative morphology of the mechanism of flight in the Lepidoptera. Unpublished thesis, Harvard University. 245 pp.

1957. The ventral intersegmental thoracic muscles of cockroaches. Smithsonian Misc. Coll. 131(11): 1–30.

1959. Spinasternal musculature in certain insect orders. Smithsonian Misc. Coll. 137: 117–56.

Czihak, G. 1953. Beiträge zur Anatomie des Thorax von *Sialis flavilatera* L. Oesterreich. zool. Zeitschr. 4: 421–48.

Kelsey, L. P. 1957. The skeleto-motor mechanism of the dobson fly, *Corydalus cornutus*. Part II. Pterothorax. Cornell Agric. Expt. Sta. Mem. 346: 1–40.

Maki, T. 1938. Studies on the thoracic musculature of insects. Mem. Fac. Sci. Agric. Taihoku Imper. Univ. 24: 1–343.

Pringle, J. W. S. 1957. Insect Flight. Cambridge Univ. Press. viii+133 pp.

Weber, H. 1924. Das Thorakalskelett der Lepidopteren. Zeitschr. Anat. und Entwickl. 73: 277–331.

1928. Die Gliederung der Sternopleuralregion des Lepidopterenthorax. Eine vergleichende morphologische Studie zur Subcoxaltheorie. Zeitschr. wiss. Zool. 131: 181–254.

TAXONOMICAL STUDIES ON THE LARVAE OF THE GENUS PSOROPHORA IN THE UNITED STATES WITH PARTICULAR REFERENCE TO THE COMMON SPECIES OF THE SUBGENUS GRABHAMIA (DIPTERA: CULICIDAE)[1]

ROBERT A. HEDEEN[2,3]

ABSTRACT

Characters are noted and keys given (1) to distinguish the four larval instars of all *Psorophora* species in the United States, (2) to distinguish the three subgenera in all larval instars, and (3) to separate three of the four North American species of subgenus *Grabhamia* in their early instars, and all of them in the fourth instar.

Mosquitoes of the genus *Psorophora* are widespread throughout the Americas and adjacent islands. They are more prevalent in the tropics, but a few species extend well into the temperate zone. At the present writing 12 species have been recorded as definitely occurring in the United States. Adults of the genus may be separated from those of other genera occurring in this country by the following characteristics: the absence of setae on the postnotum; the trilobate condition of the scutum; the presence of both spiracular and postspiracular bristles; the second marginal wing cell more than half as long as its petiole. The fourth-instar larvae of this genus resemble those of the genus *Aedes* but may be easily distinguished by the fact that the anal segment is always ringed by the dorsal plate and some of the tufts of the ventral brush penetrate the ventral margin of the plate. The characteristics of the male terminalia are quite variable in the various subgenera and are usually not used to separate the mosquitoes of this genus from those of other genera.

The genus *Psorophora* is subdivided into three subgenera, *Psorophora* with two species, *Janthinosoma* with six species, and *Grabhamia* with four species. The subgenera are readily distinguished in the adult stage by characteristics of the females and of the male terminalia. Prior to this work no attempt had been made to distinguish all of the subgenera in the larval stage. The objectives of this investigation have been to study features by which the instar of all species of the genus could be determined, subgeneric distinction in all larval instars, and specific determination in all instars of the three common species of the subgenus *Grabhamia*.

THE PRESENT STUDY

In this work complete series of the following species were examined: *Psorophora* (*Psorophora*) *ciliata*, *P.* (*P.*) *howardii*, *P.* (*Grabhamia*) *confinnis*, *P.* (*G.*) *signipennis*, *P.* (*G.*) *discolor*, *P.* (*J.*) *cyanescens*, *P.* (*J.*) *ferox*, *P.* (*J.*) *longipalpis*. First- and second-instar specimens of *P.* (*J.*) *horrida*, *P.* (*J.*) *varipes*, and *P.* (*J.*) *johnstonii*

[1]Accepted for publication February 11, 1959.

[2]Captain, Medical Service Corps, USA, Entomology Section, Department of Preventive Medicine, Army Medical Service School, Fort Sam Houston, Texas.

[3]The author is indebted to Miss Thelma L. Ford, Entomology Department, Walter Reed Army Institute of Research, Washington, D. C., who prepared the illustrations.

were not available for study. Several female specimens of *P.* (*J.*) ***mexicana*** were reported by Joyce (1945) from the vicinity of Brownsville, Cameron County, Texas. Subsequent collections have not been made. For this reason ***mexicana*** is not believed to be established in the United States and is not considered in this paper.[4] Though not all instars of some species of *Janthinosoma* were studied, it is the writer's opinion that the distinguishing characters pointed out for this subgenus will apply equally well to the species not examined in all instars.

Larval specimens of some of the species were obtained from eggs deposited in the laboratory. Specimens of other species were collected in nature shortly following a rain. At first, specimens obtained in either manner were isolated in individual containers. When ecdysis occurred the cast skin was removed and preserved. In this manner the instar of each larva was easily determined by recording the number of times it shed its skin. When distinctive features of a particular stage or species were noted from a study of the cast skins they were tested on specimens of which the instar was only suspected. After the tentative determination of a living specimen was made, it was allowed to continue development until the accuracy of the determination was ascertained. By this method it was possible to find definite characters for distinguishing the various stages and species studied.

Dodge (1946) constructed two keys by which the genera of mosquitoes found in the United States could be distinguished in the first larval instar. This writer has found that these keys, based on the characters of the so-called egg burster and other structures, are capable of distinguishing all members of this genus examined in the first instar.

The first instar of this genus may be distinguished from the other instars by the presence of the egg burster and the absence of the ventral brush. These features are pointed out by Marshall (1938) and by Dodge as being diagnostic of the first instar of all genera of mosquitoes.

The second instar of all species of mosquitoes is probably more difficult to distinguish than any other stage. Usually it differs from the third instar in only minor variations. The characteristics of the so-called stirrup-shaped piece of the siphon were used in this study to distinguish between second- and third-instar specimens. In the third instar of the species of this genus, the stirrup-shaped piece bears two anterior tooth-like projections on the ventral arm. In the second instar these projections are absent in the specimens studied.

The third instar is easily distinguished from the fourth instar by the characteristics of the anal or sclerotic plate. In the third instar the anal plate does not completely surround the anal segment and in the fourth instar the anal segment is encircled by the plate. Observations of the writer indicate that this feature may be used to differentiate the third and fourth instar of all species of mosquitoes that have the anal segment completely encircled by the dorsal plate in the fourth instar.

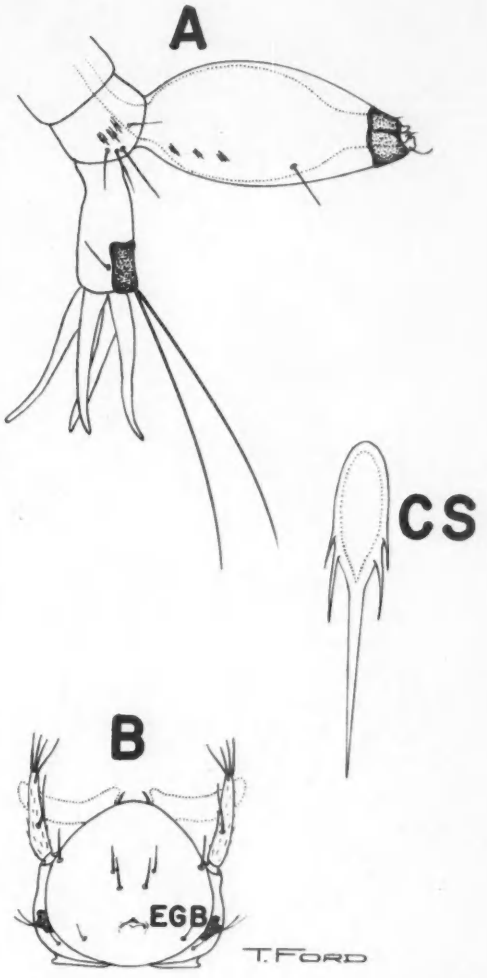


FIG. 1.—*Psorophora signipennis*, first instar. A, Terminal segments. B, Head. EGB, Egg-burster. CS, Comb scale.

A key by which the instar of all species in this genus may be determined is included as Key 1.

THE SPECIES OF THE SUBGENUS *Grabhamia*

In this study all members of the subgenus *Grabhamia* found in the United States (with the exception of the rare *P.* (*G.*) ***pygmaea***, which is

[4]Dr. R. B. Eads, of the Texas State Department of Health, also shares this opinion (personal communication, 1957).

restricted to southern Florida) were examined in all instars. In an attempt to determine the variations that might exist within a species, specimens from several different localities were used when possible in preparing the descriptions. The following represents localities from which specimens of various instars used by the writer in this specific study were collected: *P. discolor*: TEXAS: Austin, Camp Bullis, Del Rio, Fort Hood, Fort Worth, Carrizo Springs, Ozona, Fredericksburg, Junction, Sheffield, Sonora. ARKANSAS: Brinkley. MEXICO: Piedras Negras, Nuevo Laredo. *P. signipennis:* TEXAS: Austin, Camp Bullis, Fort Hood, Fort Bliss, Shepherd

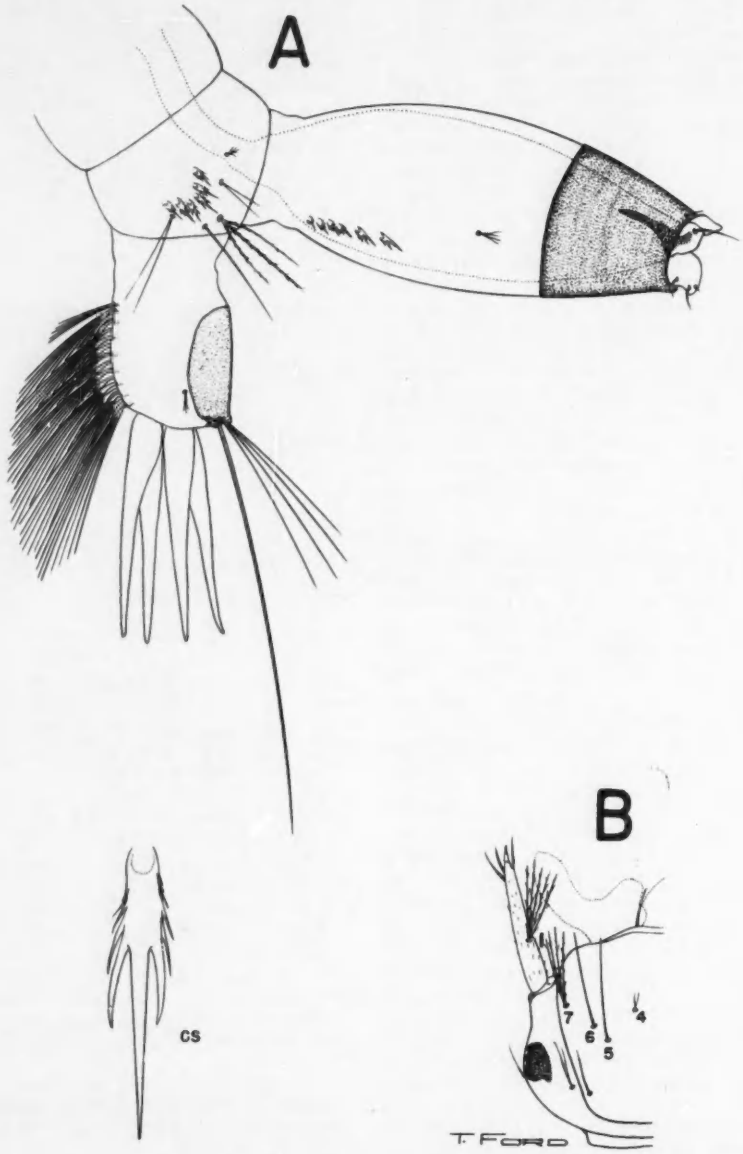


FIG. 2.—*P. signipennis*, second instar. A, Terminal segments. CS, Comb scale. B, Head: (1), antennal tuft; (4), postclypeal hair; (5), upper frontal hair; (6), lower frontal hair; (7), preantennal hair.

Air Force Base, Fort Worth, Junction, Fredericksburg, Sonora, Del Rio, Quemado, Palo Pinto, Sheffield. *P. confinnis*: TEXAS: Austin, Corpus Christi, Palmetto State Park, Fort Worth, Fort Hood, Camp Bullis, Raymondville Junction, Ozona, Sheffield, Sonora, Glen Rose, Palo Pinto, Del Rio, Liberty. ARKANSAS: Little Rock, Hot Springs, Monticello. TENNESSEE: Jonesboro. LOUISIANA: Norco. GEORGIA: Fort McPherson.

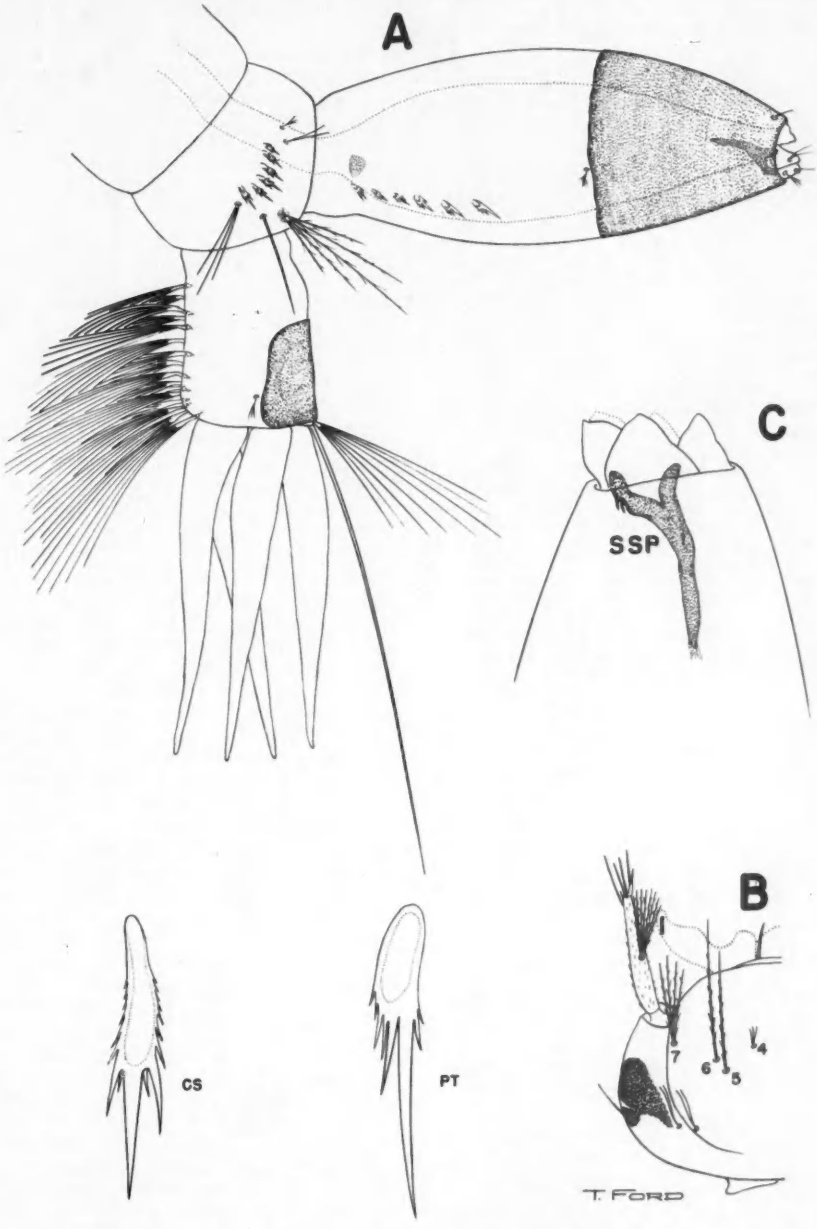


FIG. 3.—*P. signipennis*, third instar. A, Terminal segments. C, Apex of siphon. SSP, Stirrup-shaped piece. B, Head and associated structures. CS, Comb scale. PT, Pecten tooth.

FIRST INSTAR.—Species of this subgenus, excepting *P. pygmaea* which was examined only in the fourth instar, can be distinguished in the first instar. *P. discolor* differs from *P. signipennis* and *P. confinnis* in several major respects. The subventral tuft of the siphon is a feature by which *discolor* may be readily separated from either *signipennis* or *confinnis* in this instar. This hair tuft in *discolor* consists of single or double hair on each side of the siphon that is longer than the median width of the siphon. *Signipennis* and *confinnis* possess a subventral

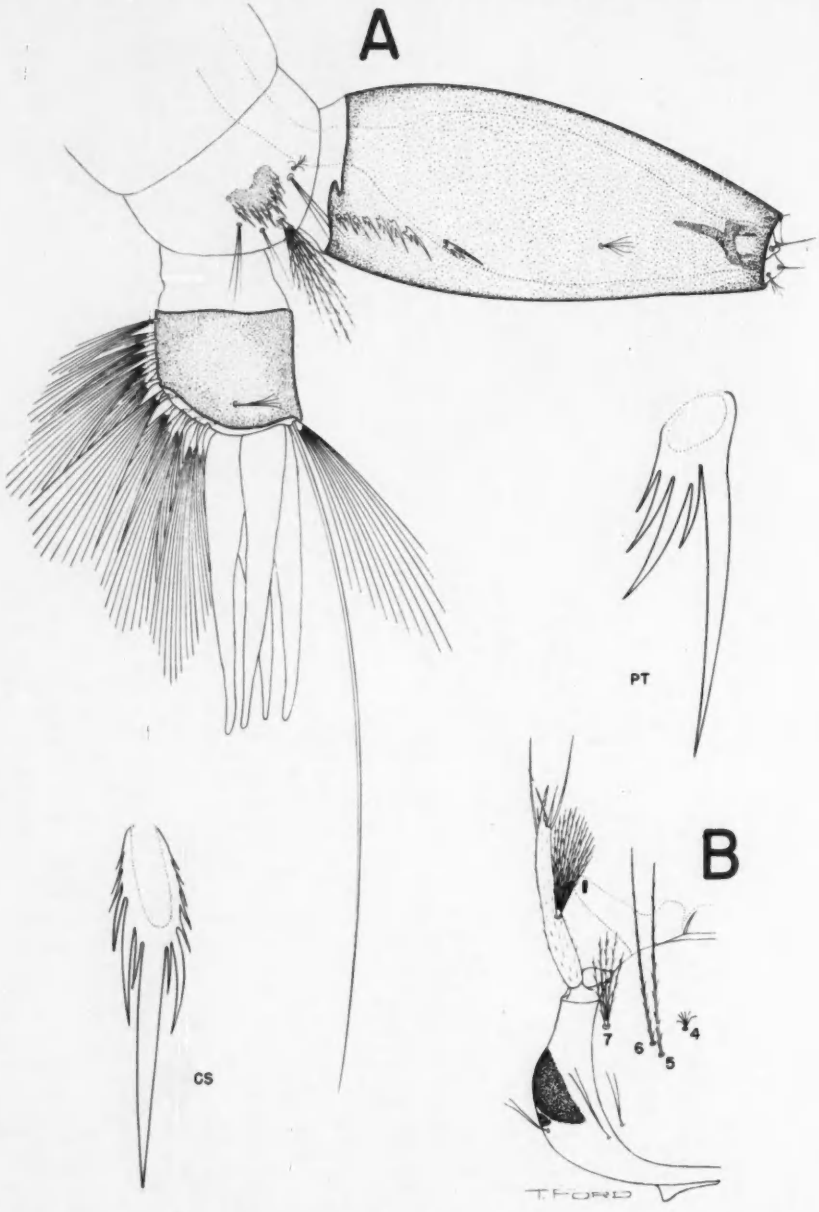


FIG. 4.—*P. singipennis*, fourth instar. A, Terminal segments. B, Head and associated structures. CS, Comb scale. PT, Pecten tooth.

tuft which is composed of a single hair on each side of the siphon that is much shorter than the median width.

P. signipennis and *P. confinnis* are rather difficult to distinguish in this instar. The insertion of the antennal tuft (1) was used, however, with a fair degree of success. Usually, the antennal tuft of *P. signipennis* is inserted on the basal half of the antenna, while *P. confinnis* usually has this tuft inserted at the middle of the antenna.

SECOND INSTAR.—The second instar of *P. discolor* is again more readily distinguished from *confinnis* and *signipennis* by the use of the subventral tuft. In this instar the tuft of *discolor* is multiple and longer than the median width of the siphon, whereas it is shorter than the median width of the siphon in *signipennis* and *confinnis*.

P. signipennis may be separated from *P. confinnis* in the second instar by the number of branches in the upper and lower frontal head hairs (5 and 6). *P. signipennis* has single frontal head hairs, while *P. confinnis* has frontal head hairs two to four branched.

THIRD INSTAR.—Many features exist by which the three species may be distinguished in this instar. The characteristics of the subventral tufts are still very good in separating *discolor* from *signipennis* and *confinnis*, so for the sake of consistency it has been used again in the third instar as a key character. In this instar the subventral tuft of *discolor* is very much longer than the median width of the siphon, while in *signipennis* and *confinnis* it is less than one-half the median width of the siphon in length.

The site of insertion of the subventral tuft easily separates *signipennis* from *confinnis* in this instar. The tuft is inserted basally to the apical cap of the siphon in *signipennis*, and in *confinnis* it is inserted within this cap.

FOURTH INSTAR.—Several morphological features have been utilized in the key for distinguishing the individual species in this instar. Considerable variation has been noted in *signipennis* (Hedeen 1954), and frequently it is difficult to make a positive identification. It is the writer's belief, however, that with the use of this key the investigator will be able to identify all fourth-instar larvae of the subgenus *Grabhamia* found in the United States—if any variations they exhibit fall within the ranks of those previously noted by this and other writers.

The morphological features referred to in this paper are explained by figures 1, 2, 3, and 4, which illustrate, respectively, the first, second, third, and fourth instars of *P. signipennis*.

1. KEY TO INSTARS: GENUS *PSOROPHORA*

1. Egg burster present; ventral brush absent . . *First Instar*
   Egg burster absent; ventral brush present 2
2. Stirrup-shaped piece with no small projections on edge of ventral arm . . . . . *Second Instar*
   Stirrup-shaped piece with one or two small projections on edge of ventral arm 3
3. Dorsal plate not completely surrounding anal segment . . . . . *Third Instar*
   Dorsal plate completely surrounding anal segment *Fourth Instar*

2. KEY TO SUBGENERA

First Instar

1. Mouth brushes stout, modified for grasping; head quadrate . . . . . **Psorophora**
   Mouth brushes hair-like, not modified for grasping; head rounded . . . . . **Grabhamia**
   Janthinosoma

Second Instar

1. Mouth brushes stout, modified for grasping; head quadrate; pecten teeth numerous, 18 or more **Psorophora**
   Mouth brushes hair-like, not modified for grasping; head rounded; pecten teeth few, less than eight . . . 2
2. Pecten teeth two to four (usually three) . **Janthinosoma**
   Pecten teeth five or six (usually six) . . . . **Grabhamia**

Third Instar

1. Mouth brushes stout, modified for grasping; head quadrate; pecten teeth 18 or more . . . . **Psorophora**
   Mouth brushes hair-like, not modified for grasping; head rounded; pecten teeth less than eight 2
2. Upper frontal head hairs (5) double; *or*, upper frontal hairs single, antennal hair tuft (1) weak, two- or three-branched . . . . . **Janthinosoma**
   Upper frontal head hairs single or multiple, not double; antennal hair tuft strong, five- to many-branched . . . . . **Grabhamia**

Fourth Instar

1. Mouth brushes stout, modified for grasping; head quadrate; pecten teeth 18 or more . . . . **Psorophora**
   Mouth brushes hair-like, not modified for grasping; head rounded; pecten teeth fewer than eight 2
2. Antennae large, longer than head, subapical spines placed near tip; *or*, antennae shorter than head, antennal tuft weak, two- to four-branched, subapical spines placed near tip . . . . . **Janthinosoma**
   Antennae small, shorter than or as long as head, antennal tuft strong, eight- to many-branched; *or*, antennae longer than head, subapical spines placed near middle, antennal tuft strong, more than four-branched . . . . . **Grabhamia**

3. KEY TO SPECIES OF SUBGENUS *GRABHAMIA*

First Instar

1. Subventral tuft of siphon a long, single or double hair on each side, longer than median width of siphon . . . . . **P. discolor**
   Subventral tuft of siphon a single hair on each side, shorter than median width of siphon 2
2. Antennal tuft (1) inserted on basal half of antenna **P. signipennis**
   Antennal tuft inserted at middle of antennae . . . . . **P. confinnis**

Second Instar

1. Subventral tuft a long, multiple hair on each side, longer than median width of siphon . . . **P. discolor**
   Subventral tuft a small, multiple hair on each side, shorter than median width of siphon 2
2. Upper and lower frontal head hairs (5 and 6) single **P. signipennis**
   Upper and lower frontal head hairs two- to four-branched . . . . . **P. confinnis**

Third Instar

1. Subventral tuft a long, multiple hair on each side, longer than median width of siphon . . . **P. discolor**
   Subventral tuft a small, multiple hair on each side, shorter than median width of siphon 2
2. Subventral tuft inserted basally to apical cap of chitin of siphon . . . . . **P. signipennis**
   Subventral tuft inserted within apical cap of chitin of siphon . . . . . **P. confinnis**

Fourth Instar

1. Subventral tuft as long as siphon; siphon not inflated or chitinized to base; antennae inflated, much longer than head; preantennal hair (7) double ..... **P. discolor**
   Not as above 2
2. Upper and lower frontal head hairs (5 and 6) multiple ..... **P. confinnis**
   Upper and lower frontal head hairs usually single, occasionally individual hairs double or triple, rarely all four hairs double or triple 3
3. Hair of lateral valve of siphon less than half as long as apical width of siphon; upper and lower frontal head hairs usually single; known in U. S. only from Florida ..... **P. pygmaea**
   Hair of lateral valve of siphon more than half as long as apical width of siphon; upper and lower frontal head hairs usually single, but not infrequently double or triple; in Central and Southwestern States **P. signipennis**

REFERENCES CITED

Dodge, H. R. 1946. Studies upon mosquito larvae. Abstracts of Doctoral Dissertations, No. 50. Ohio State University Press.

Hedeen, R. A. 1954. The identification of the larva of *Psorophora* (*Grabhamia*) *signipennis* (Coquillett). Mosquito News 14(3): 143–5.

Joyce, C. R. 1945. The occurrence of *P. mexicana* (Bellardi) in the United States. Mosquito News 8: 102–5.

Marshall, J. F. 1938. The British Mosquitoes. London: British Museum (Natural History). 341 pp.

UTILIZATION OF FOOD PLANTS BY THE MIGRATORY GRASSHOPPER, MELANOPLUS BILITURATUS (WALKER)[1] (ORTHOPTERA: ACRIDIDAE), WITH SOME OBSERVATIONS ON THE NUTRITIONAL VALUE OF THE PLANTS[2]

D. S. SMITH

Regional Research Station, Canada Department of Agriculture, Lethbridge, Alberta

ABSTRACT

Grasshoppers were fed individually on either wheat, western wheat grass, or oats for 40 days after hatching. Survival was highest on wheat and lowest on western wheat grass, and the rate of development was equal on these two and lowest on oats. The amounts of wheat and western wheat grass consumed were approximately equal and were twice that of oats. The final weights of the grasshoppers fed on oats were about one-third less than the weights on the other two foods. Utilization for the 40-day period was 32% on each of the three foods, but during the first 5 days it was 81% on western wheat grass, 65% on wheat, and 54% on oats. The efficiency of conversion of food to body tissue was 38% for oats, 32% for wheat, and 27% for western wheat grass, and was negatively correlated with the amount of food utilized. The various criteria indicate that wheat is a good food; that oats is a poor food only because the grasshoppers do not eat enough; and that western wheat grass is a poor food, possibly because of a deficiency in nutrients.

Many plant species are available to a grasshopper, or to any other phytophagous insect, but generally few are suitable as food. It has been shown, for instance, that dandelion and wheat are good foods for survival and development of *Melanoplus bilituratus* (Walker) whereas Russian thistle, oats, and many native grasses are poor foods (Pfadt 1949; Smith et al. 1952). There has been considerable speculation on the reason for this difference, but very little research on it has been done. The purpose of this work was to study the utilization of different food plants by *M. bilituratus* in order to provide some answers to this question and to increase our knowledge of the relationship between this insect and the food plants of its habitat.

MATERIAL AND METHODS

Newly hatched nymphs of *M. bilituratus* were reared singly in cages on one of three food plants and records were kept of survival, time of development, amount of food eaten, amount of faeces, and the gain in weight of the insects.

Insects.—Insects were hatched from eggs collected in the field in the fall of the previous year. The eggs were kept at 5° C. until needed.

Cages.—Two types of vertical, cylindrical cages were used. Those for small nymphs were 5-inch lengths of 1½-inch-diameter glass tubing with cheesecloth closing the top. For larger nymphs, which required more ventilation, 5-inch by 1¾-inch plastic vials were used. Windows 4 inches by 1 inch were cut in opposite sides of the vials and covered with plastic mesh. The cages were corked at the bottom and the food was inserted

[1] *M. mexicanus* of authors in part. A. R. Brooks. Acridoidea of Southern Alberta, Saskatchewan, and Manitoba (Orthoptera). Canadian Ent. Suppl. 9, 1958.

[2] Contribution No. 114, Regional Research Station, Canada Department of Agriculture, Lethbridge, Alberta, being part of a dissertation submitted to the University of Minnesota for the degree of Doctor of Philosophy. The author is indebted to Dr. A. C. Hodson, University of Minnesota, for suggestions and criticisms and to R. R. Forster, of this station, for assistance with the rearing of the insects. Accepted for publication February 13, 1959.

through a hole in the cork, the cut end of the plant protruding below. Each cage was placed over a hole in a board above a tray of water, with the cut end of the plant in the water. The cork floors of the cages were covered with wax paper, renewed at each feeding, to facilitate collection of faeces and to discourage nibbling on the cork.

Food.—Three plants were used as food: Renown wheat (*Triticum aestivum* L.), Ajax oats (*Avena sativa* L.), and western wheat grass (*Agropyron smithii* Rydb.). These were chosen because they are generally available in the insects' habitat and because of their relative suitabilities as food. Wheat has been shown to be a good food and oats a poor one (Smith et al. 1952), and there have been some indications that western wheat grass was of intermediate value (Pfadt 1949).

The plants were grown in a greenhouse in vermiculite and supplied with a "complete" nutrient solution by an automatic subirrigation system. Air pressure, turned on by a time-controlled solenoid valve, forced the solution from carboys into the vermiculite for 2 minutes every 6 hours. When the air pressure was turned off, the solution drained back into the carboys and allowed aeration of the vermiculite. The same nutrient solution was used for all plants. It was composed of:—

KH_2PO_4	—1 mM per l.
$MgSO_4.7H_2O$	—2 mM per l.
KNO_3	—5 mM per l.
$Ca(NO_3)_2.4H_2O$	—5 mM per l.

plus 1 ml. per litre of the following micronutrient solution:

H_3BO_3	—2.8 gm. per l.
$MnSO_4.4H_2O$	—2.1 gm. per l.
$ZnSO_4.7H_2O$	—0.2 gm. per l.
$CuSO_4.5H_2O$	—0.08 gm. per l.
$H_2MoO_4.H_2O$	—0.02 gm. per l.

Periodically a freshly mixed 0.5 percent solution of ferrous sulphate was added directly to the vermiculite. The solution in the carboys was replaced every 2 weeks, and every 2 or 3 days distilled water was poured through the vermiculite into the carboys to compensate for evaporation and to prevent accumulation of salts in the vermiculite. The plants were grown from November until June, with artificial supplementation of natural light during the winter. The wheat and oats were used approximately 4 weeks after seeding whereas the slower-growing western wheat grass was used 6 to 8 weeks after seeding.

Rearing.—The insects were weighed and placed in a cage within 24 hours of hatching and supplied immediately with food. The food supply was replenished every second or third day in the cages of the younger nymphs and every day in those of the older nymphs and adults.

Because only 40 to 50 insects could be handled at one time, rearing was carried on continuously for several months and new nymphs were started as death or maturation of others made space available. As far as possible, nymphs from each hatching were allocated to all of the three food plant treatments. Each insect received only one type of food.

The food supplied to each insect was weighed to the nearest ½ milligram on a torsion balance immediately after being cut. Other samples of fresh food were taken to determine moisture content. When fresh food was placed in a cage, the uneaten food was removed, dried in a vacuum oven for 48 hours at 98° C., and weighed.

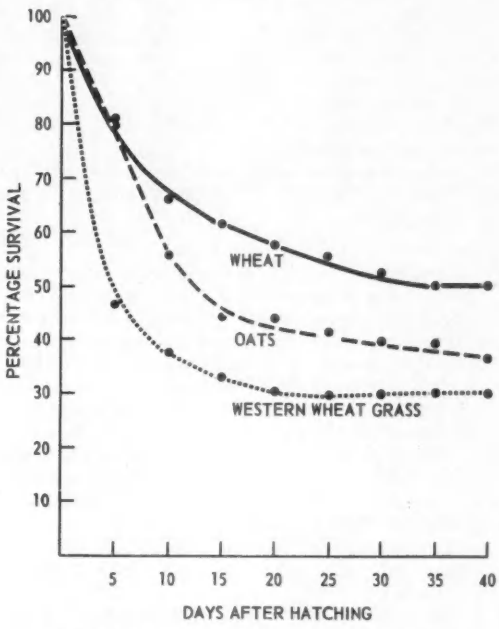


FIG. 1.—Survival of *M. bilituratus* on three foods.

Every fifth day each insect was weighed, transferred to a clean cage, and given a fresh supply of food. The faeces from each insect accumulated over each 5-day period were dried and weighed.

Additional grasshoppers that were reared singly on each food for 10, 20, or 30 days were weighed, killed by heat, and dried *in vacuo* at 98° C. to determine the moisture content.

The amount of food consumed by each insect was calculated by subtracting the dry weight of the food removed from the cage from the calculated dry weight of the food offered. The amount of food utilized was the amount consumed less the dry weight of the faeces. Percentage utilization was calculated as:

$$\frac{\text{food consumed—faeces}}{\text{food consumed}} \times 100$$

Percentage efficiency of conversion was calculated as:

$$\frac{\text{gain in dry weight}}{\text{food utilized}} \times 100$$

The rearing was carried on in a room in which the temperature was controlled at 30±1° C. and the relative humidity at 45±3 percent. The room was lighted continuously by 40-watt fluorescent tubes.

The insects were reared for 40 days or as much longer as necessary to bring them to the adult stage, and data were tabulated for each 5-day period.

Students' "t" tests indicated no significant differences between the sexes in the amounts of food consumed and utilized and in the weight gains during the whole nymphal period or during the last 5 days only. Consequently, data for both sexes are combined.

Some preference trials were conducted and the methods used for these will be detailed with the results below.

RESULTS

Survival.—The highest survival at the end of the test was obtained with wheat and the lowest with western wheat grass (table 1). The great majority of those that died on western wheat grass did so in the first 5 days, as shown in fig. 1. Mortality rapidly decreased after this and no deaths occurred after 25 days. On wheat and oats survival declined more gradually but continued to decline until the end of the 40 days. These differences in survival are consistent with those reported by Pfadt (1949) and Smith et al. (1952) for this grasshopper.

Nymphal Development.—Nymphs of *M. bilituratus* fed on oats took almost one-third longer to reach the adult stage than did those fed on wheat and western wheat grass (table 1). Pfadt (1949) observed a nymphal period of 42 days in this species feeding on western wheat grass compared with 35 days on wheat. The wheat he used was laboratory-grown but the western wheat grass was collected in the field and so was probably more mature than that used here.

M. bilituratus is usually described as having five nymphal instars, but an extra one is not uncommon (Shotwell 1930). In the present work an extra instar appeared between the regular third and fourth instars in 85 percent of those reared on oats and in 47 percent and 40 percent of those reared on wheat and western wheat grass.

Growth.—The weights of the grasshoppers fed on wheat and western wheat grass for 40 days were the same and were both significantly higher than the weight of those fed on oats for 40 days (table 1). The oat-fed grasshoppers were almost one-third lighter.

Food Consumption, Utilization, and Conversion.—The consumption and utilization of the different foods and the gains in weight of the grasshoppers are given in table 2. A ninth 5-day period is shown for oats because the nymphal stages extend into this period. The standard deviations show the great range of individual variation in the insects.

The consumption of oats was approximately one-half that of the other foods over the 40-day period. Consideration of the amounts consumed during the nymphal period revealed only that the consumption of oats was still the lowest, 462 mg., compared with 567 mg. of wheat and 612 mg. of western wheat grass.

The utilization percentages over the full 40-day period were the same for all foods, 32 percent, so that the amounts of food utilized on the different diets were in the same proportions as the amounts consumed. Consideration of only the average percentage utilization for the full period masks the striking differences that were apparent in the early stages (fig. 2). Utilization was highest in the first 5-day period, and distinctly different among the 3 foods. The values rapidly decreased in the early periods, particularly on wheat and western wheat grass, levelled off in the fourth, fifth, and sixth periods, and then decreased again.

The average efficiencies of conversion for the whole period were 38 percent for oats, 32 percent for wheat, and 27 percent for western wheat grass. Fig. 3 shows how the conversion efficiencies changed during the different 5-day periods. They were very low at the beginning, increased to a peak, and then declined. Here again marked differences existed among the foods in the early stages. The percentage efficiencies for western wheat grass, wheat, and oats for the first period were in the ratio 1:2:3.

Table 1.—Effect of three foods on growth and development of *M. bilituratus*.

Food	Initial no. insects	Percent Survival after 40 days	Duration nymphal period (days±s.e.)	Live weight after 40 days (mg.±s.e.)
Wheat	96	50.0	34.1±0.6	283.0±12.7
Western wheat grass	145	29.7	34.9±0.4	286.3± 9.8
Oats	82	36.6	43.8±0.6	176.6± 7.2

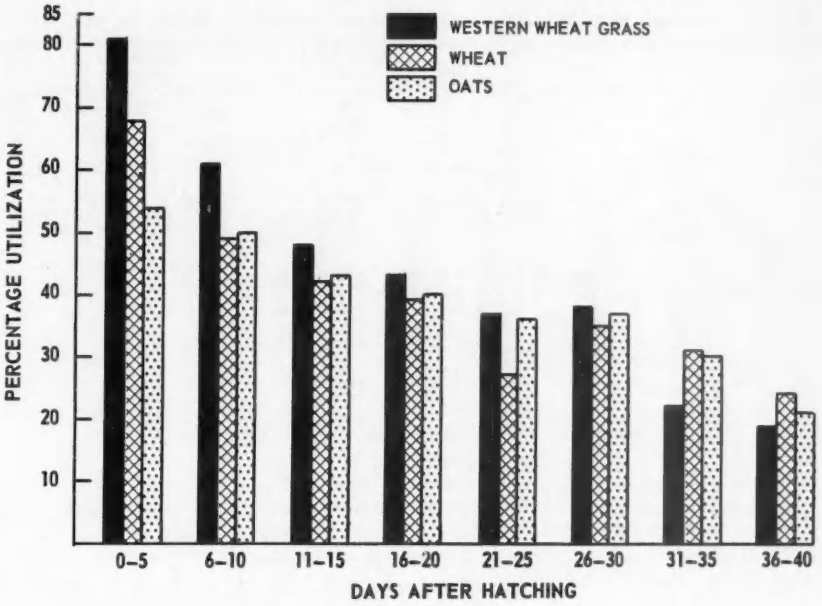


FIG. 2.—Utilization of three foods by *M. bilituratus*.

The original data for individual insects showed a tendency toward a negative correlation between the efficiency of conversion and the total amount of a particular food utilized during the 40 days following hatch. Correlation coefficients were −.546 for wheat, −.722 for western wheat grass, and −.364 for oats, the first two being significant ($P<.01$), the third not significant. Covariance analysis (Snedecor 1946) of the mean efficiencies of conversion on the different foods after adjusting them to a basis of equal food intake showed that these means did not differ significantly.

Food-Plant Preferences.—To determine whether the grasshoppers showed a preference for any of the plants, two methods were used. In one, five grasshoppers starved for 24 hours were placed in one of the rearing cages, in which there were approximately equal amounts of the three plants, inserted through three holes in the bottom cork. The grasshoppers were allowed to feed for 24 hours or less and then the amount of feeding from each plant was estimated visually. From several such observations on newly hatched nymphs the amount of oats eaten in 24 hours was estimated to be generally less than 1 percent of that available whereas the amounts of wheat and western wheat grass eaten were each about 10 percent. Observations on 20-day-old nymphs after a 7-hour feeding interval similarly revealed a consumption of generally less than 1 percent and always less than 5 percent of the oats. Wheat consumption was about 10 to 15 percent and western wheat grass 5 to 10 percent.

In the other method the same cage arrangement was used, and counts were made after set intervals of the number of grasshoppers that were feeding on each plant, resting on a plant, and resting on the cage. Table 3 gives some typical results.

With both methods a decided preference was shown for wheat and western wheat grass. There may have been a slight preference for wheat over western wheat grass among the older nymphs, but none was discernible in the younger ones. Pfadt (1949) showed that wheat was greatly preferred by *M. bilituratus* and selected over all the other 12 plants used except dandelion; western wheat grass was one of the least preferred. As mentioned previously, Pfadt used field-collected and probably more mature western wheat grass than was used here, and this may account for its lower acceptability. Skoog (reported in Scharff 1954) indicated that western wheat grass was one of the preferred food plants of *M. bilituratus*. In the present work oats was much the least preferred food and this agrees well with the low consumption of this plant and with its low value for survival and egg production shown by Smith et al. (1952).

Dry Weights of Materials.—The average dry weights of the food plants as a percentage of the wet weights with standard errors were:—

Wheat	9.0 ± 0.16
Western wheat grass	13.4 ± 0.35
Oats	7.8 ± 0.13

Table 2.—Average consumption, utilization, and weight gain in *M. bilituratus* on three foods.

Food plant	Five-day periods									Totals Periods 1–8	Standard deviation
	1	2	3	4	5	6	7	8	9		
	(mg. dry weight)										
Food consumed											
Wheat	11.8	21.7	41.0	71.7	102.8	139.3	178.6	148.0		714.9	189.7
Western wheat grass	15.0	22.4	39.3	69.4	110.7	182.6	172.3	198.4		810.1	148.9
Oats	5.2	10.1	16.4	27.6	43.8	80.0	86.8	103.1	89.1	373.0**	70.9
Food utilized											
Wheat	8.0	10.6	17.4	27.7	28.2	49.2	55.1	35.5		231.7	69.8
Western wheat grass	12.1	13.7	18.7	29.5	40.8	69.5	37.7	37.7		259.7	40.6
Oats	2.8	5.0	7.0	11.0	15.8	29.6	26.3	21.5	16.6	119.0**	24.7
Gain in weight											
Wheat	1.2	2.7	5.8	8.3	15.3	13.2	15.6	8.1		70.2	19.2
Western wheat grass	0.9	1.5	3.4	7.0	12.6	16.7	16.0	10.8		68.9	15.4
Oats	0.6	1.1	2.5	3.7	5.7	8.8	9.5	11.5	7.2	43.4**	9.9

**Significantly different (1 percent level) from other two food plants (Fisher-Behrens' test).

Dry weights of individual grasshoppers were measured at 10, 20, 30, and 40 days after hatching. Differences between individuals within an age class were as great as the differences between classes so that all individuals are averaged in the following table, which gives the dry weight as a percentage of the wet weight with the standard error:—

M. bilituratus fed on wheat ..... 25.2±0.69
M. bilituratus fed on western wheat grass ..... 24.3±0.80
M. bilituratus fed on oats ..... 25.3±0.47

The dry matter content of the grasshoppers appears to be independent of the dry matter content of the food.

DISCUSSION

Food Consumption, Utilization, and Conversion.—Various "indices of consumption" have been set up for standardizing the reporting of food consumption by different insect species (Lafon 1951; Legay 1957). The simplest is probably the best for comparative purposes; that is, the amount consumed during all or a large part of the nymphal (or larval) period, divided by the weight gain during this period. In the present work the ratios of food eaten to unit weight gain on a dry weight basis for the average nymphal period are 8.97, 9.13, and 10.40 for wheat, oats, and western wheat grass, respectively. A similar calculation applied to Rubtzov's (1932) figures, and assuming a dry matter content of 25 percent for both insects and food, gives a value of 14.40 for *Chorthippus albomarginatus* on *Bromus inermis*. For *Schistocerca gregaria* (Davey 1954) feeding on mixed grasses the value is 4.55. A still lower value of 2.34 was obtained for *Carausius morosus* feeding on ivy (Lafon 1951). So even within the Orthoptera different species on different foods show a wide range of consumption in attaining a unit body weight.

As Lipke and Fraenkel (1956) point out in a recent review, data on utilization of food in insects are scarce. Legay (1957) has summarized the data on silkworms and Lafon (1951) has summarized most of that for other insects. Values for Orthoptera reported in the literature vary from 33 percent utilization for *S. gregaria* adults on endive (Chauvin 1946) to 66 percent for the same species in the fifth instar on endive (Brennière et al. 1949).

Table 3.—Preference of *M. bilituratus* for three foods.

Position	Numbers of insects			
	A[a]		B[b]	
	Resting	Feeding	Resting	Feeding
Wheat	30	0	17	10
Western wheat grass	48	2	13	8
Oats	2	0	16	2
Cage	158	0	84	0

[a]Newly hatched nymphs. Sum of eight observations at 15-minute intervals.

[b]Twenty-day-old nymphs previously fed on a mixture of the three plants plus dandelion and starved for 24 hours before test. Sum of six observations extending over 6 hours.

The few reports dealing with early nymphal or larval stages all give very high values of utilization for this period (Davey 1954; Evans 1939; Hiratsuka 1920). These values, coupled with the low conversion efficiency in the early stages, indicate a very high energy requirement. This is particularly noticeable with first-instar grasshoppers feeding on western wheat grass. For every 15 mg. of the wheat grass eaten 12 mg. are retained, but only 1 mg. of these 12 is incorporated into body tissue, the other 11 being used to produce the energy necessary for metabolism. The

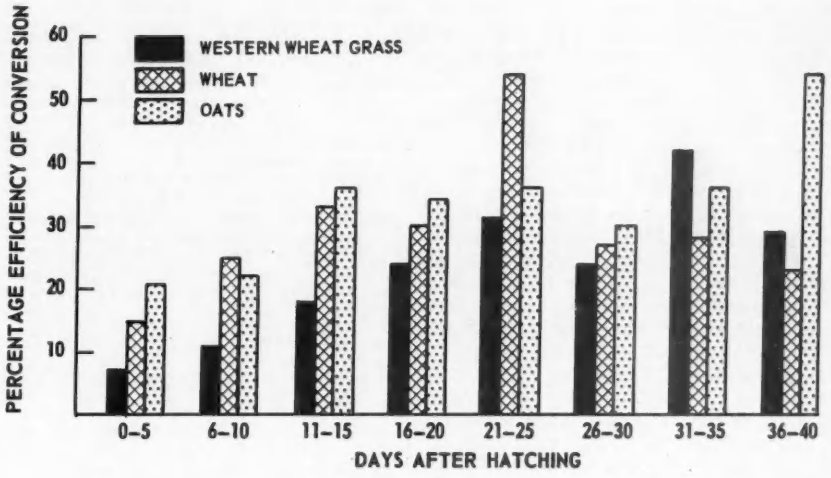


FIG. 3.—Efficiency of conversion of three foods to body tissue by *M. bilituratus*.

conversion efficiency, however, increases gradually as development proceeds, reaching a maximum about 10 days before adult emergence on wheat, 5 days on oats, and immediately before emergence on western wheat grass.

Nutritional Value of Plants.—There are various opinions as to why some plants are preferred to others by certain insects and why some plants appear to be better foods than others. Fraenkel (1951, 1953) considers that the leaves of all plants contain the same basic nutritional substances and the selection of plants for food is not made on the basis of any nutritional need. He suggests that "it is the presence or absence of odd chemical substances in which the plants differ, such as glucosides, essential oils, alkaloids, saponins, or tannins, which render the plant a suitable or unsuitable food." Dethier (1954) also believes that nutritionally unimportant stimuli are predominantly responsible for plant preferences.

Painter (1951), however, considers that plants and different parts of the same plant may differ nutritionally and states "The absence of necessary vitamins, amino acids, or fatty acids in the part of the plant on which the insect feeds, offers a possible explanation of the effects of some resistant plants on insects." Kennedy (1951) thinks that there may be a definite causal relationship between preference and nutritional differences.

There is no doubt that an attractant sometimes is the cause of preference, particularly where there is a marked attraction to one plant or group of plants. Such occurs with larvae of *Pieris* and mustard oil glucosides in *Cruciferae* (Verschaffelt 1910). It seems possible, however, that a nutrient may be the cause of preference at other times; indeed Thorsteinson (1953) has found that in some circumstances where an attractant is definitely involved, the feeding response can be enhanced by adding nutrients to the attractant material. It is also possible that all green leaves do not contain all the necessary nutrients and that some plants are poor foods, or are "resistant," because of a nutritional deficiency.

In this work, wheat was a reasonably suitable food for *M. bilituratus* while oats was unsuitable. Mortality was lowest on wheat, the developmental period was short, the adult weight attained was high, and the grasshoppers showed a decided preference for it. On the other hand, on oats the mortality was greater, development slower, the adult weight was lower than that attained on wheat, and oats was the least preferred of the three plants. Nevertheless, although a smaller amount of oats was eaten than of the other plants, this amount was used to just as good advantage in growth. The amount of oats consumed during the nymphal period per gram of final dry weight was the same as for wheat. The efficiency of conversion of oats was at least equal to that of wheat. So it would seem probable that oats was just as nutritious as wheat and was a poor food simply because not enough of it was eaten. Further evidence of this is the extra instar that appeared in 85 percent of the grasshoppers raised on oats, twice as frequently as on the other two foods. Extra instars are commonly found in insects that do not get sufficient food (Wigglesworth 1950). The absence of an attractant or the presence of a repellent made oats unattractive to the grasshopper, as the preference tests indicated.

Western wheat grass, on the basis of time of

development and weight attained, appeared to be as good a food as wheat. The preference for it shown by the grasshoppers was the same as for wheat. But the high mortality suffered by those that fed on it indicated that it should be classed as an unfavorable food. Seventy-five percent of those that died on this plant did so in the first 5 days (fig. 1); the comparable figure for wheat was 40 percent and for oats 28 percent. But in these first 5 days the grasshoppers on western wheat grass ate more than did those on wheat. Those that survived these 5 days on western wheat grass but died shortly thereafter ate just as much and showed the same percentage utilization as those that survived throughout. Thus there was no question of the insects not eating enough because of a repellent or the lack of an attractant. In the first 10 days the weight gain on 37.4 mg. of western wheat grass consumed was only 2.4 mg. whereas on 33.5 mg. of wheat consumed the gain was 3.9 mg. (table 2). With the very high rate of utilization in the early stages, this means that a relatively large amount of food was being processed, most of it not being used for growth but apparently just for energy. The survivors continued to show a high rate of consumption of western wheat grass so that, in eventually reaching the same weight as those fed on wheat, they ate about 15 percent more.

In view of the high consumption and utilization of western wheat grass, it seems unlikely that a toxic factor is involved unless it resembles that found by Beck in corn (Beck 1957; Beck and Stauffer 1957) where the toxic effect of the "toxic factor" was lessened by another substance, a sugar. In corn a decreased feeding response was associated with this factor as would be expected with a poison, but there was no decreased response with western wheat grass. Also, survival was much higher on western wheat grass, 82 percent after 3 days and 47 percent after 5 days, than during starvation under the same conditions, 47 percent after 2½ days and nil after 3½ days (Smith 1951), which makes the presence of toxic substance seem unlikely.

The other possibility is that western wheat grass is deficient in some substance or substances needed by the grasshopper and only a small percentage of those feeding on it could overcome this deficiency. Even to these the food was still somewhat inadequate, as indicated by an average rate of conversion lower than that for wheat during most of the nymphal period. Thus western wheat grass must be considered as a plant that is nutritionally inadequate for *M. bilituratus* rather than one on which feeding is inhibited by nutritionally unimportant factors.

REFERENCES CITED

Beck, S. D. 1957. The European corn borer, *Pyrausta nubilalis* (Hübn.), and its principal host plant. IV. Larval saccharotrophism and host plant resistance. Jour. Econ. Ent. 50: 247–50.

Beck, S. D., and **J. F. Stauffer.** 1957. The European corn borer, *Pyrausta nubilalis* (Hübn.), and its principal host plant. III. Toxic factors influencing larval establishment. Jour. Econ. Ent. 50: 166–70.

Brennière, J., H. Jover, and **R. de Malmann.** 1949. Sur la nutrition de quelques Orthoptères. Rev. Path. Vég. et Ent. Agric. France 28: 134–40.

Chauvin, R. 1946. Notes sur la physiologie comparée des Orthoptères. IV. Le coefficient d'utilisation digestive, le rythme d'excrétion et le transit intestinal. Bull. Soc. Ent. France 51: 24–29.

Davey, P. M. 1954. Quantities of food eaten by the desert locust, *Schistocerca gregaria* (Forsk.) in relation to growth. Bull. Ent. Res. 45: 539–51.

Dethier, V. G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution 8: 33–54.

Evans, A. C. 1939. The utilization of food by certain lepidopterous insects. Trans. Roy. Ent. Soc. London 89: 13–22.

Fraenkel, G. 1951. The nutritional value of green plants for insects. Trans. IXth Internatl. Congr. Ent. 2: 90–100.

1953. Insects and plant biochemistry. The specificity of food plants for insects. Trans. XIVth Internatl. Congr. Zool. 383–7.

Hiratsuka, E. 1920. Researches on the nutrition of the silkworm. Bull. Imp. Sericult. Expt. Sta. Japan 1: 257–315.

Kennedy, J. S. 1951. Host plant selection in Aphididae. Trans. IXth Internatl. Congr. Ent. 2: 106–13.

Lafon, M. 1951. Quelques documents sur l'appétit et la consommation alimentaire chez les insectes. Ann. Nutrition et Alimentation 5: 485–504.

Legay, J. M. 1957. La prise de nourriture chez le ver à soie. Ann. Inst. Natl. Recherche Agron. ,Sér. C, Ann. Épiphyt. Numéro hors série.

Lipke, H., and **G. Fraenkel.** 1956. Insect Nutrition. Ann. Rev. Ent. 1: 17–44.

Painter, R. H. 1951. The role of nutritional factors in host plant selection. Trans. IXth Internatl. Congr. Ent. 2: 101–5.

Pfadt, R. E. 1949. Food plants as factors in the ecology of the lesser migratory grasshopper *Melanoplus mexicanus* (Sauss.). Univ. Wyoming Agric. Expt. Sta. Bull. 290.

Rubtzov, I. A. 1932 (On the amount of food consumed by locusts.) [in Russian; English summary.] Trudy Zashchite Rastenii, Ser. 1, Entomol., No. 2: 31–40.

Scharff, D. K. 1954. The role of food plants and weather in the ecology of *Melanoplus mexicanus mexicanus* (Sauss.). Jour. Econ. Ent. 47: 485–9.

Shotwell, R. L. 1930. A study of the lesser migratory grasshopper. U. S. Dept. Agric. Tech. Bull. 190.

Smith, D. S. 1951. Unpublished monthly report. Jan.-Feb. (p. 7.) Field Crop Insect Laboratory, Lethbridge, Alberta.

Smith, D. S., R. H. Hanford, and **W. Chefurka.** 1952. Some effects of various food plants on *Melanoplus mexicanus mexicanus* (Sauss.) (Orthoptera: Acrididae). Canadian Ent. 84: 113–7.

Snedecor, G. W. 1946. Statistical Methods. 4th ed., Chap. 12. Ames: Iowa State College Press.

Thorsteinson, A. J. 1953. The chemotactic responses that determine host specificity in an oligophagous insect (*Plutella maculipennis* (Curt.) Lepidoptera). Canadian Jour. Zool. 31: 52–72.

Verschaffelt, E. 1910. The cause determining the the selection of food in some herbivorous insects. Proc. Acad. Sci. Amsterdam 13: 536–42.

Wigglesworth, V. B. 1950. Principles of Insect Physiology. 4th ed. (p. 43). London: Methuen and Co., Ltd.

FEEDING CULEX TARSALIS ON OUTDATED WHOLE HUMAN BLOOD THROUGH ANIMAL-DERIVED MEMBRANES (DIPTERA: CULICIDAE)[1]

I. BARRY TARSHIS[2]

Department of Entomology, University of California, Los Angeles

ABSTRACT

The highest feeding rates were obtained with 4- to 7-day-old mosquitoes that remained in the feeding chambers 3 to 4 hours and fed in an ambient temperature of 25° C., through Silverlight membranes. The outdated human blood was held at 4° C. until needed, then warmed to the desired temperature just prior to its use. Somewhat lower feeding percentages obtained in several experiments were probably due to use of mosquitoes that were too young, or to the presence of males and/or excessive numbers of females in the feeding chambers. Mosquitoes deprived of sugar for 48 hours and of water for 24 hours before the blood meal fed better and ingested more blood than mosquitoes that were allowed sugar and water until just prior to membrane feeding. Partially fed mosquitoes ingested from 0.29 to 0.75 mg. of blood, fully engorged ones 1.12 to 2.44 mg., when fed through Silverlight, Nearkid, Zephir, and Fourex membranes.

The findings by Rodhain and co-workers in 1912 that tsetse flies could become infected with the organisms of sleeping sickness by feeding on infective blood through rat-skin membranes and, in the same year, the development of an in vitro technique by Hindle and Merriman for feeding ticks through rat diaphragms on a variety of solutions, gave subsequent investigators a valuable tool for carrying out research on the transmission of bacterial, viral, protozoan and helminthic micro-organisms; on insect physiology, nutrition and behavior.

The membrane-feeding technique has been fully utilized in carrying out research with mosquitoes. One of the first studies on membrane-feeding of mosquitoes was that of Sen (1917). In his studies on the role of blood in ovulation in *Stegomyia* (=*Aedes*) *scutellaris* (Walker), he was unsuccessful in feeding the mosquitoes through albumin-cloth, tender plantain shoots, soaked gelatin, tough cloth, and childrens' balloons. Gordon (1922) was able to feed *Aedes calopus* (Meig.) (=*A. aegypti*) through the skin of a bat, but he found that the mosquitoes never fed to repletion through this type of membrane. However, Woke (1937) was successful in feeding *Aedes aegypti* (Linn.) through rat-skin membranes upon whole blood and certain fractions of it. Similarly, Greenberg (1949) was able to feed large numbers of *A. aegypti* on a wide variety of artificial fluids through Baudruche capping membranes. In her studies on the distribution of certain liquids in the esophageal diverticula and stomach of *Anopheles* Meigen, *Aedes* Meigen, and *Culex* Linn., Trembly (1952) successfully carried out these studies by feeding these mosquitoes on blood through Baudruche capping and chicken-skin membranes. Shambaugh (1954), in studies on the effect of various foods on digestive enzyme elaboration, fed *A. aegypti* through Baudruche capping membranes. Of 14 membranes screened for use in feeding *A. aegypti* on heparinized beef blood, Tarshis (1957b) found Nearkid, Fourex, hamster skin, Silverlight, and rabbit-skin membranes to give the highest feeding rates.

The employment of the membrane-feeding technique for carrying out studies on the transmission of arthropod-borne infections has been used with a good degree of success. In their studies on the transmission of dengue fever by *A. aegypti*, St. John et al. (1930) infected these mosquitoes with dengue virus by feeding the mosquitoes through guinea-pig-skin membranes on suspensions of dengue-infected *A. aegypti* in blood. In 1935 Knowlton and Rowe, in their investigative work on equine encephalomyelitis, infected species of *Aedes*, *Anopheles*, *Theobalaia* Neveu-Lemaire, and *Culex* by feeding them upon suspensions of diseased brain through animal mesentery bags. In the transmission of *Plasmodium falciparum* (Welch) by *Anopheles elutus* Edwards, Yoeli (1938) was able to infect the mosquitoes by feeding them through rabbit-skin membranes on infected blood. Similarly, in studies with *Plasmodium gallinaceum* Brumpt, *A. aegypti* were infected after being fed on infected blood through chicken skin (Bishop and Gilchrist 1944, 1946) and through hog-gut sausage casings (Eyler 1952). Kartman (1953), in his studies on factors influencing infection of the mosquito with *Dirofilaria immitis* (Leidy), fed *A. aegypti* on blood containing microfilariae through hog-gut saugage casings.

The current paper reports on five different membranes and an apparatus used for feeding *Culex tarsalis* Coquillett, and gives results of experiments with the membranes and apparatus.

[1]Accepted for publication February 27, 1959.

[2]Special thanks are extended to Mr. Arthur Bartley of the Physics Department machine shop, University of California at Los Angeles, for the fabrication of the membrane feeding apparatus.

Table 1.—Comparative results of feeding starved *Culex tarsalis* on outdated human blood through various animal-derived membranes

Membranes used	Age of mosquitoes (Days)	Blood temp. (°C.)	Ambient temp. (°F.)	Feeding time (Hrs.)	Females per chamber	Males per chamber	Number examined			Total number fed	Percent fed of total used	Percent engorged of total fed
							Unfed	Fed				
								Partially	Engorged			
Zephir	2–4	34	77	4	99	14	41	12	46	58	58.5	79.3
Nearkid	2–4	34	77	4	68	10	27	13	28	41	60.2	68.2
Silverlight	2–4	34	77	4	151	9	65	31	55	86	56.9	63.9
Silverlight	2–6	34	75	4	132	10	43	12	77	89	67.4	86.5
Naturalamb	2–6	34	75	4	81	7	26	22	33	55	67.9	60.0
Fourex	2–6	34	75	4	68	8	22	9	37	46	67.6	80.4
Silverlight	4–7	34	77	4	77	2	10	15	52	67	84.6	77.6
Silverlight	4–7	34	77	4	95	2	8	18	69	87	91.5	79.3
Silverlight	6–7	34	76	3	221	19	59	46	116	162	73.3	71.6
Naturalamb	6–7	34	76	3	108	10	21	50	37	87	80.5	42.5
Nearkid	6–7	34	76	3	142	15	36	59	47	106	74.6	44.3

MATERIALS AND METHODS

Membrane-feeding apparatus.—The membrane-feeding apparatus (fig. 1) consists of (1) a thermostatically controlled water bath, (2) chambers to hold the blood, and (3) feeding chambers, to which membranes are attached, to hold the insects to be fed.

A standard, commercially manufactured water bath (Precision, Catalogue No. 66648) is used to heat the blood and to hold it at a constant temperature.

The feeding chamber consists of two main parts (figs. 2, 3, 5), a screen cylinder that allows room for the mosquitoes to fly about before and after feeding, and a membrane holder. Two identically designed but different-sized screened cylinders were made. The smaller one, made of #30-mesh stainless steel wire cloth, is 2½ inches in diameter and 6¾ inches high. The larger one, made of #30-mesh bronze screen cloth, is 4 inches in diameter and 7⅝ inches high. A metal plate with a 1-inch diameter hole is soldered to the top of each screen cylinder. The hole is covered with two pieces of slitted dental dam placed one on top of the other so that the slits are at right angles to each other. This opening in the top of the cylinder facilitates the introduction of mosquitoes with an aspirator tube without danger of escapes. A metal ring is soldered to the outside bottom edge of each screen cylinder to give rigidity to the cylinder and for fitting it onto the plexiglas membrane holder.

The plexiglas membrane holder for the 2½-inch diameter cylinder is ¼-inch thick, 1⅜ inches high, and with an outside diameter of 2½ inches. There is a ⅛-inch-wide lip, ¼-inch below the top outside edge of the membrane holder, to allow for fitting it into the bottom of the screen cylinder. The membrane is secured to the membrane holder with a plexiglas ring, ¼-inch high and 3/16-inch thick, with an outside diameter of 2⅞ inches. After the membrane is secured by the ring over the bottom of the holder, the excess membrane is trimmed off, and the ring and the membrane edges are covered with ¾-inch-wide plastic, pressure-sensitive tape. The tape not only holds the membrane securely to the membrane holder, but also insures against blood leaking into the holder. Pressure-sensitive tape No. 473 (Transparent plastic film) and pressure-sensitive tape No. 474 (Flame-resistant plastic film), manufactured by the Minnesota Mining and Manufacturing Company, have been found excellent for securing the membranes to the membrane holders.

A ⅛-inch-high adaptor ring, with an inside diameter of 2½ inches and an outside diameter of 3¾ inches, fits over the membrane holder and holds the assembled feeding chamber (cylinder and membrane holder) upright in the blood chamber. The adaptor ring also has a ¼-inch hole to hold a thermometer.

The 4-inch-diameter blood chamber for the 2½-inch feeding chamber is made of ¼-inch thick plexiglas. The cup is 3¼ inches high. To form an adaptor ring support, 1/16 inch of the inside surface of the top 2 inches of the blood chamber is trimmed away.

The plexiglas membrane holder for the 4-inch diameter cylinder is ¼ inch thick, 1¾ inches high, and has an outside diameter of 4 inches. There is a 5/16-inch-high, ⅛-inch-wide lip cut around the top outside edge of the membrane holder to allow for it fitting into the bottom of the screen cylinder (fig. 2). The membrane is secured to the holder with a plexiglas ring, ¼-inch high and 3/16 inch wide with an outside diameter of 4⅜ inches. The membrane is secured to the plexiglas holder in the same manner as described for the smaller holder.

An adaptor ring, with an inside diameter of 4 inches, an outside diameter of 5¼ inches, and

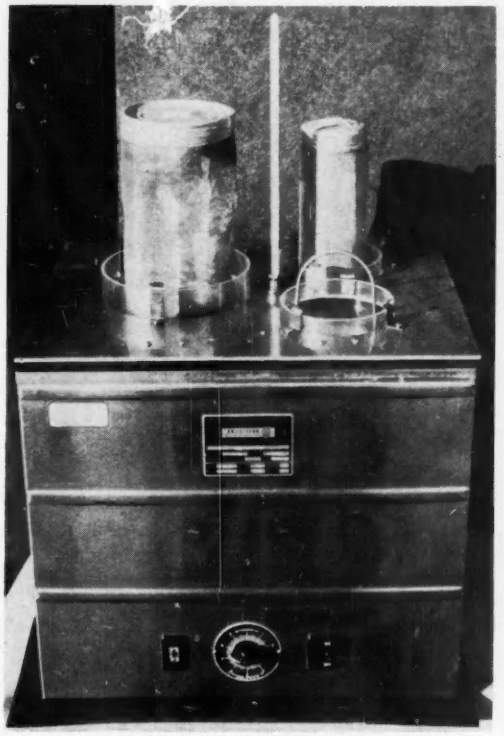


FIG. 1.—Completely assembled membrane feeding apparatus.

a height of ⅛ inch, fits over the membrane holder and holds the assembled feeding chamber upright in the blood chamber. The adaptor ring also has a ¼-inch hole for a thermometer.

The blood chamber for the 4-inch feeding chamber is made of ¼-inch-thick plexiglas and has an outside diameter of 5½ inches. The cup is 3½ inches high. To form an adaptor ring support, 1/16-inch of the inside top 2¼ inches is trimmed away.

An aluminum plate (fig. 4) ⅛ inch thick, 12¼ inches wide and 15¼ inches long, with two 4-inch diameter holes and one 5-inch diameter hole, fits on the top of the water bath. A 1-inch-wide, ¼-inch-thick rubber gasket is attached to the under surface of the aluminum plate where it rests upon the top of the water bath. Two stainless steel strips, 1/16 inch thick and 1⅞ inches wide, are attached to the underside of the aluminum plate and form supports 2½ inches below the under surface of the plate for the blood chambers which are inserted into the aluminum plate holes. Each blood chamber is further secured to the plate by three copper spring clips bolted to the top edge of each opening in the plate.

Membranes.—Silverlight, Nearkid, Zephir and Fourex membranes are commercially prepared and were purchased from Julius Schmid, Inc., 423-439 West 55th Street, New York 19, N. Y. Naturalamb, also a commercially prepared membrane, was purchased from the Young's Rubber Corporation, 145 Hudson Street, New York 13, N. Y.

Blood.—Outdated, citrated whole human blood, obtained from the Clinical Laboratory, University of California, Los Angeles, was used for feeding the mosquitoes. The blood was stored in the original containers in a refrigerator held at 4° C. When needed, the blood was taken from the container, warmed to the desired temperature, and placed in the blood chamber of the feeding apparatus where a constant temperature was maintained throughout the feeding period.

Mosquitoes.—The mosquitoes were reared from eggs by standard rearing methods. The adults were held in holding cages at room temperature. In most cases the mosquitoes were deprived of apple 48 hours and water 24 hours prior to the blood meal. Female mosquitoes used for the feeding experiments were collected with an aspirator-suction tube from the holding cages. Though care was taken to select only females, males sometimes inadvertently were picked up and placed into the mosquito chambers along with the females. All mosquitoes were fed in a lighted room, and unless otherwise indicated, were allowed to feed during the morning hours.

At the conclusion of each feeding experiment, the feeding chamber was removed from the blood

FIG. 2.—Unassembled membrane feeding chamber. Upper left, screened cylinder; upper right, plexiglas membrane holder; lower left, plexiglas adaptor ring; lower right, plexiglas ring to hold the membrane on membrane holder.

Table 2.—Results of feeding starved and nonstarved *Culex tarsalis*, 4 to 7 days old, on outdated human blood through Silverlight membranes.[a]

	Total mosquitoes used	Number unfed	Number fed		Total fed	Percent fed of total used	Percent engorged of total fed
			Partially	Engorged			
Starved	172	18	33	121	154	89.5	78.5
Nonstarved	163	58	41	64	105	64.3	60.9

[a]Feeding time 4 hours; blood temperature 34° C.; ambient temperature 77° F.

chamber and the blood washed from the membrane and membrane holder. All mosquitoes not to be retained alive were killed with chloroform by placing the entire feeding chamber into a chloroform killing chamber for about 15 minutes, or until all the mosquitoes were dead. A 3000-ml. size beaker with chloroform-impregnated cotton in the bottom served well as a killing jar. The beaker was capped with heavy duty aluminum foil and foil was placed over the cotton to prevent damage to the plexiglas by the chloroform. The dead mosquitoes were next transferred from the feeding chambers to petri dishes and then examined under a microscope to separate the unfed from the fed mosquitoes. It was found that a dissecting microscope with a substage mirror was best for this purpose. The heavy glass stage of the microscope was removed and replaced with a heavy piece of cardboard, the same size as the glass stage, with a center hole cut to the exact size for holding a 4-inch petri dish lid.

By directing a light onto the mirror of the dissecting microscope and transmitting the light from the mirror up through the petri dish and bodies of the mosquitoes, one can separate the unfed, partially fed and fully engorged mosquitoes with ease. Mosquitoes with completely blood-filled digestive tracts were tabulated as fully engorged. Those with lesser quantities of blood, no matter how minute, were designated as partially fed. By using the transmitted light technique one can detect even minute quantities of blood in the digestive tracts of fed mosquitoes, but when light is directed from above the stage onto the mosquitoes, the digestive tracts become darkened and it is most difficult to determine whether a mosquito has ingested blood or not. Of course, the distention of the abdomen in a fed mosquito also can be used as a criterion for feeding, but this method cannot be relied upon, for the ingestion of small quantities of blood will not cause any distention.

In working with mosquitoes that must be kept alive, the mosquitoes in the feeding chamber are first anesthetized with CO_2 for an initial knock-down, to facilitate their removal from the feeding chambers. They are then transferred to a continuous anesthetizing chamber (Tarshis 1957a) which is substituted for the glass stage on the dissecting microscope. By allowing CO_2 to flow through this chamber, and using transmitted light to illuminate the digestive tracts of the mosquitoes, one can separate the unfed from the fed mosquitoes very readily. Once the feeding tabulations were made, the partially fed and fully engorged mosquitoes were weighed to determine the quantities of blood that they had ingested.

RESULTS AND DISCUSSION

Culex tarsalis were able to feed through the

Table 3.—Quantities of blood ingested by *Culex tarsalis* fed on outdated human blood through various animal-derived membranes

Membranes used	Unfed			Partially fed			Engorged			Blood ingested per mosquito	
	Number weighed	Total weight (mg.)	Average weight (mg.)	Number weighed	Total weight (mg.)	Average weight (mg.)	Number weighed	Total weight (mg.)	Average weight (mg.)	Partially fed (mg.)	Engorged (mg.)
Silverlight	99	169	1.70	58	144	2.45	192	731	3.80	0.75	2.10
Naturalamb	47	84	1.57	41	102	2.48	60	241	4.01	0.91	2.44
Fourex	22	31	1.40	9	18	2.00	37	122	3.29	0.60	1.89
Nearkid	36	72	2.00	59	135	2.29	47	147	3.12	0.29	1.12

Mosquitoes 2 to 7 days of age.
No apple 48 hours and no water 24 hours prior to blood meal.
Blood temperature 34°C., Ambient temperature 76°F.
Feeding time 4 hours.

FIG. 3.—Membrane feeding chamber completely assembled and ready for placement in blood chamber.

membranes on out-dated whole human blood which was held at a temperature of 34° C. This substantiated the findings of previous studies by the writer (Tarshis 1957b, 1958a, 1958b) that showed that *Xenopsyllus cheopis* (Rothschild), *Ornithodoros moubata* (Murray), *Ornithodoros savignyi* (Audouin), and *A. aegypti* could be fed on blood through membranes held at 34° C.

Tarshis (1958a, 1958b) found that ambient temperatures between 19° and 30° C. yielded good feeding for *X. cheopis*, *O. moubata*, *O. savignyi*, and *A. aegypti*. In feeding *C. tarsalis* through membranes during the current investigation, good feeding rates were obtained at an ambient temperature of around 25° C.

Allowing the mosquitoes to remain in the feeding chambers from 3 to 4 hours resulted in highest feeding percentages. The writer (1957b) also found this to be the case in feeding experiments with *A. aegypti*.

Feeding results with *C. tarsalis* with five different membranes are presented in table 1. The somewhat lower feeding rates obtained with some of the membranes could be due to the fact that the mosquitoes used were too young, the feeding chambers were overcrowded and/or the males present in the feeding chambers prevented the females from feeding. In the two most successful experiments with Silverlight membranes it will be noted that the mosquitoes were 4 to 7 days old, there were few males in the chambers, and there were fewer female mosquitoes in each chamber than in the other experiments utilizing Silverlight membranes. The writer also found in membrane-feeding experiments with *A. aegypti* that when all three of the above-mentioned conditions were optimum, high feeding rates were obtained, not only with Silverlight, but with all those currently tested with *C. tarsalis*.

In arthropod transmission experiments with mosquitoes a number of investigators (Russell 1931; Merrill and Tenbroeck 1934; Burgess and Young 1944) showed that mosquitoes fed best when deprived of sugar and water for a period of 1 to 2 days prior to the blood meal. Contrariwise, Bar-Zeev and Smith (1959), in studies on repellents with *A. aegypti*, were able to obtain fairly high feeding rates with nonstarved mosquitoes. In the current studies starved and nonstarved *C. tarsalis* were fed through Silverlight membranes. From the results obtained, as shown in table 2,

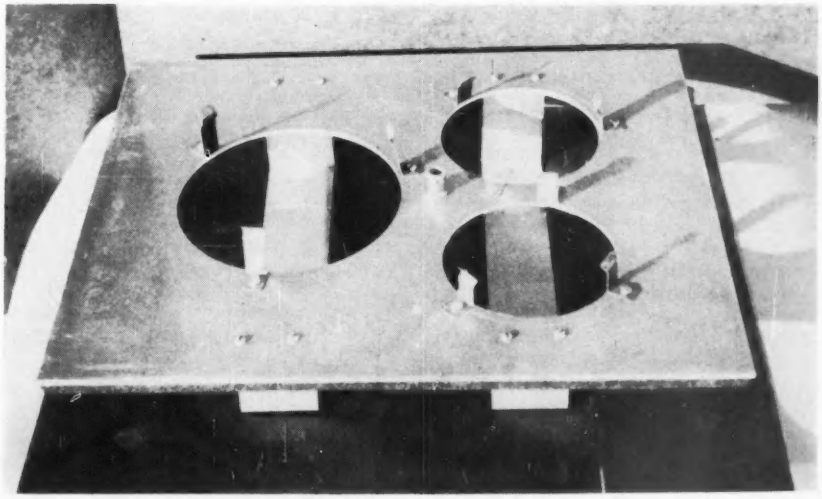


FIG. 4.—Aluminum plate for holding blood and feeding chambers in water bath.

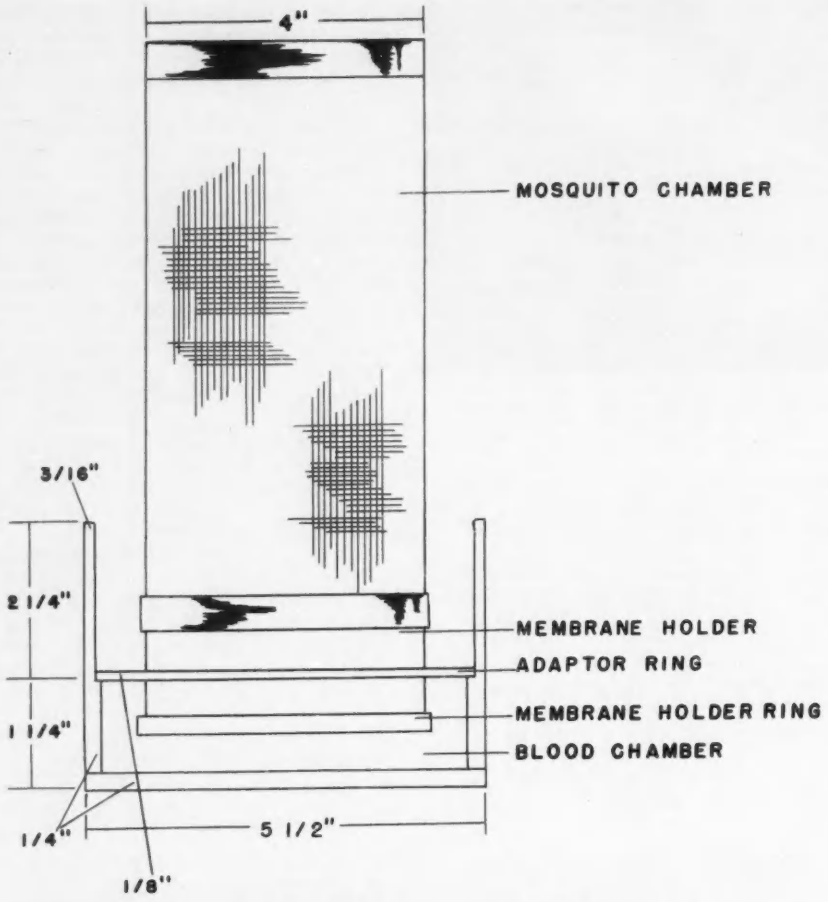


FIG. 5.—Schematic drawing of large feeding and blood chambers showing placement of feeding chamber on adaptor ring support within blood chamber. To form the adaptor ring support, 1/16 inch of the inside surface of the upper 2¼ inches of the blood chamber is trimmed away.

the starved mosquitoes fed better than the non-starved. This was also shown to be true in experiments with *A. aegypti* (Tarshis 1957b).

Studies on the quantity of blood ingested by various species of mosquitoes when fed on animals have shown that *A. aegypti* ingests from 0.7 to 6.0 milligrams of blood (Hovanitz 1947; Day and Bennetts 1954; Lang and Wallis 1956), *A. minimus* Theobald around 1.0 milligram (Laurel 1934), *A. vexans* (Meigen) 2.07 milligrams, and *A. aldrichi* Dyar and Knab 2.10 milligrams (Stage and Yates 1936).

In the current experiments partially fed *C. tarsalis* ingested from 0.29 to 0.75 milligrams of blood and the fully engorged from 1.12 to 2.44 milligrams. The results of these experiments are shown in table 3. Comparative studies were not made to determine the quantity of blood ingested by *C. tarsalis* when allowed to feed on laboratory animals.

REFERENCES CITED

Bar-Zeev, M., and **C. M. Smith.** 1959. Action of repellants on mosquitoes feeding through treated membranes or on treated blood. Jour. Econ. Ent. 52(2): 263–7.

Bishop, A., and **B. M. Gilchrist.** 1944. A method for collecting sporozoites of *Plasmodium gallinaceum* by feeding infected *Aedes aegypti* through animal membranes. Nature 153(3893): 713–4.

1946. Experiments upon the feeding of *Aedes aegypti* through animal membranes with a view to applying this method to the chemotherapy of malaria. Parasitology 37: 85–100.

Burgess, R. W., and **M. D. Young.** 1944. Methods of handling and feeding *Anopheles quadrimaculatus* upon malaria patients. Jour. Natl. Malaria Soc. 3(4): 241–7, 3 figs.

Day, M. F., and **M. J. Bennetts.** 1954. A review of problems of specificity in arthropod vectors of plant and animal viruses. Canberra, Australia: Div. Ent., Commonw. Sci. and Indust. Res. Org. 3+172 pp., 4 figs.

Eyles, D. E. 1952. Studies on *Plasmodium gallinaceum*. II. Factors in the blood of the vertebrate host influencing mosquito infection. Amer. Jour. Hyg. 55(2): 276–90.

Gordon, R. M. 1922. Notes on the bionomics of *Stegomyia calopus*, Meigen, in Brazil. Part II. Ann. Trop. Med. and Parasitol. 16(4): 425–39, 2 figs.

Greenberg, J. 1949. A method of artificially feeding mosquitoes. Mosquito News 9: 48–50.

Hindle, E., and **G. Merriman.** 1912. The sensory perceptions of *Argas persicus* (Oken). Parasitology 5(3): 203–16.

Hovanitz, W. 1947. Physiological factors which influence infection of *Aedes aegypti* with *Plasmodium gallinaceum*. Amer. Jour. Hyg. 45(1): 67–81.

Kartman, L. 1953. Factors influencing infection of the mosquito with *Dirofilaria immitis* (Leidy, 1856). Exptl. Parasitol. 2(1): 27–78.

Knowlton, G. F., and **J. A. Rowe.** 1935. Handling mosquitoes on equine encphalomyelitis investigation. Jour. Econ. Ent. 28: 824–9.

Lang, C. A., and **R. C. Wallis.** 1956. An artificial feeding procedure for *Aedes aegypti* using sucrose as a stimulant. Amer. Jour. Trop. Med. and Hyg. 5(5): 915–20.

Laurel, A. G. 1934. Feeding activities of some Philippine *Anopheles*. Rev. Filipina Med. y Farm. 25(7): 286–97.

Merrill, M. H., and **C. Ten Broeck.** 1934. Multiplication of equine encephlomyelitis virus in mosquitoes. Proc. Soc. Exptl. Biol. and Med. 32(3): 421–3.

Rodhain, J., E. Pons, J. van den Branden, and **J. Bequaert.** 1912. Contribution au mécanisme de la transmission des trypanosomes par les glossines. Arch. Schiffs u. Trop. Hyg. 16: 732–9.

Russell, P. F. 1931. A method for feeding blood meals to mosquitoes, male and female. Preliminary note. Amer. Jour. Trop. Med. 11(5): 355–8.

St. John, J. H., J. S. Simmons, and **F. H. K. Reynolds.** 1930. Trasmission of the virus of dengue fever from mosquito to mosquito. Philippine Jour. Sci. 41(g): 381–5.

Sen, S. K. 1917. A preliminary note on the role of blood in ovulation in Culicidae. Indian Jour. Med. Res. 4(4): 729–53.

Stage, H. H., and **W. H. Yates.** 1936. Some observations on the amount of blood engorged by mosquitoes. Jour. Parasitol. 22(3): 298–300.

Tarshis, I. B. 1957a. An apparatus and technique for the continuous anesthetization of haematophagous insects with dry ice. Mosquito News 17(2): 83–6.

1957b. Feeding *Aedes aegypti* (L.) through animal derived membranes. Amer. Jour. Trop. Med. and Hyg. 7: 251. (Abstract.)

1958a. A preliminary study on feeding *Ornithodoros savignyi* (Audouin) on human blood through animal-derived membranes (Acarina: Argasidae). Ann. Ent. Soc. America 51: 294–9.

1958b. Feeding techniques for bloodsucking arthropods. Proc. Tenth Internatl. Congr. Ent., Montreal 1956, 3: 767–84.

Trembley, H. L. 1952. The distruibtion of certain liquids in the esophageal diverticula and stomach of mosquitoes. Amer. Jour. Trop. Med. and Hyg. 1(4): 693–710.

Woke, P. A. 1937. Effects of various blood fractions on egg production of *Aedes aegypti* Linn. Amer. Jour. Hyg. 25(2): 372–80.

Yoeli, M. 1938. Note on the experimental infection of *Anopheles elutus* with *Plasmodium falciparum* by feeding through a prepared animal membrane. Riv. Malariol. 17(1): 62–66.

BIOLOGICAL STUDY OF THE RICE WEEVIL COMPLEX[1]

E. H. FLOYD AND L. D. NEWSOM
Louisiana Agricultural Experiment Station, Baton Rouge

ABSTRACT

The large and the small rice weevils are distinct, reproductively isolated species. The name *Sitophilus oryza* (L.) is applicable to the former, *S. sasakii* (Tak.) to the latter. Coloration is variable in both, their measurements overlap, and no practical external morphological distinctions were found, but the two species differ in the eighth sternum of the female and in the shape of a sclerite on the dorsal surface of the aedeagus of the male. Reproduction of both species was least in maize (corn), next in rough rice, and greatest in grain sorghum; with *S. oryza* reproduction was greater in unpolished rice than in wheat, but with *S. sasakii* the reverse was true. When both species were confined on maize or unpolished rice, the larger species proved to be the dominant form; on wheat the smaller species became dominant. Size and color in both forms was influenced by the host.

The variability in size of the rice weevil, *Sitophilus oryza* (L.) Schönherr (=*Calandra oryza* (L.)) has been commonly attributed to the influence of the host. During the course of some control studies on this insect at Baton Rouge, Louisiana, it was observed that rough rice (palea and lemma intact) (Zenith) of an average grain moisture of 12 percent stored adjacent to heavily infested maize (*Zea mays* L.) was little damaged by this species. Many rice weevils were found in this rice, but the majority of them were dead. Live specimens were rarely found, indicating that rough rice is not a suitable host for this species.

Rough rice (Zenith) of an average grain moisture of 11.5 percent in field scale storage tests at Crowley, Louisiana, conducted concurrently with the Baton Rouge study, did not become infested by the rice weevil until after

[1]Accepted for publication March 14, 1959.

Table 1.—Crosses between the large and the small species of rice weevils held at 80°±1° F. and 65±5 percent R.H.[a]

Type of cross[b]	No. of pairs	No. females with sperm in spermatheca	No. females with no sperm in spermatheca	Percent positive matings
♂ ♀				
Large×small	70	0	70	0
Small×large	47	0	47	0
Large×large	19	18	1	95
Small×small	14	13	1	93

[a]Individuals of the large species were obtained from a laboratory culture maintained for six generations in maize, those of the small species from a laboratory culture maintained for six generations in wheat.

[b]In each cross the mean age of the individuals was 24 hours when paired, and the average time they were left together was 8 days.

several months of storage. When it did become infested the weevils were much smaller than those normally found in maize.

These observations indicated that this small weevil found at Crowley may have been a different species than the larger form commonly found in corn in Louisiana.

REVIEW OF LITERATURE

Linnaeus (1763) gave the following description of the rice weevil:

"Curculio oryza longirostris oblongus niger, elytris maculis quatuor ferrugineis, femoribus muticis. Habitat in oryzae seminibus, ab exteris regionibus allatis. Magnitudo grani oryzae, totus niger sive piceoniger, punctis cavis scaber, oblongus, subtus piceus est. Elytra striata, in singulis macula dua ferruginea, quarum prior ad basin elytri, posterior ante apicem elytri."

Motschulsky (1855) described *Sitophilus Zeamais*, which he had observed infesting corn (maize) from Cayenne at the New York Exposition during 1853. He observed that rice (apparently rough rice) exhibited in the same building was not infested during the progress of the exposition. Since he described these specimens as a new species, based on their large size, it is evident that he considered the smaller form to be the species described by Linnaeus.

According to Kiritani (1956), Sasaki as early as 1899 recognized *Calandra oryzae*[2] var. minor. Recognition of this variety was based on its comparatively small size. Also, according to Kiritani (1956), Takahashi in 1918 recognized morphological and ecological differences between *C. oryzae* and *C. oryzae* var. *minor*.

Takahashi (1928–1931) described *C. sasakii* (=*C. oryzae* var. *minor*). Elevation of var. *minor* to specific rank was based on average differences in (1) length and weight of body, (2) proportion of length to width, (3) coloration, (4) number of punctures on the prothorax, and (5) a patch on the wings.

It appears that European and American workers have been unaware until recently of the studies made in Japan.

Zacher (1922) described a large form of rice weevil, which originated in corn from LaPlata, as *Calandra oryzae* var. *platensis*. The differences which he considered sufficient to justify erection of the variety were larger size, brighter coloration, and differences in the male copulatory organ. He did not describe these differences. He was aware of the effect of host on size, but pointed out that this could not be responsible for the difference observed since specimens bred from corn from Natal and Togo were what he termed the usual rice weevil. It appears he was concerned with the same form that Motschulsky (1855) had described as *S. Zea-mais* and, like Motschulsky, considered the small rice weevil to be the Linnaean species. He also observed that *platensis* dispersed readily to fields in the vicinity of Düsseldorf by flight. He stated that all *Calandra* found flying in Düsseldorf were *C. oryzae* var. *platensis*, regardless of whether the rice weevil also occurred abundantly on stored grain in that area.

Schmidt (1925) pointed out the impossibility of determining with certainty which of the two forms was described by Linnaeus since the description by the latter was far from complete. The size of the specimen described was given as that of a rice grain. Schmidt (1925) recognized the variability in size of kernels of different varieties of rice and mentioned the fact that Linnaeus had not specified the variety used for comparison. He redescribed Motschulsky's *S. Zea-mais*, which he considered to be the same as *platensis* described by Zacher. Schmidt also pointed out that the small species observed in Europe, usually but not always in rice, was considered to be *C. oryza* L. He separated the two species according to the following description:

[2]Most subsequent writers have used the emended spelling *oryzae*, which first appeared in the second edition (1789) of Linnaeus' "Amoenitates Academicae."

"*C. oryza* L. Body small and slender; 2 to 2.8 mm (without snout); dull, sculpturing coarse, shallow and irregular, individual punctures as well as the broader, more obtuse intervals only weakly shining and almost dull. Antenna short and thick, second segment of the flagellum little longer than the third; prothorax in its greatest width as broad as it is long or somewhat narrower, laterally up to the weakly contrasting collar clearly and more evenly constricted. Penis more slender, wider in the apical half than in the basal part."

"*C. Zea-mais* Motsch. (=*platensis* Zacher). Body considerably larger and broader, 3 to 3.5 mm (without snout); shining; the spots of the wing covers sharply defined and vividly colored; punctation coarse; the individual punctures sharply penetrating and deep, shining as in the narrow and keeled intervals. Antennae longer and thinner, second segment of the flagellum nearly twice as long as the third. Prothorax in its greatest width somewhat broader than long, laterally smoothly rounded and up to the clearly contrasting collar strongly constricted. Penis of the same width and robust."

Zumpt (1935) revised the European species of *Calandra* and called attention to the variability of *C. oryzae* in size and sculpturing. He recognized only three species, *granaria* L., *oryzae* L., and *linearis* Hbst. He was unable to distinguish between *C. oryzae* L. and *C. zea-mais* Motsch. on the characters given by Schmidt (1925), and considered differences reported as representing normal variation.

Richards (1944) stated that the large and small "strains" of *C. oryzae* differed principally in size. He found that the two forms crossed with great difficulty to produce hybrids which were apparently sterile. They differed in length of life cycle at 25° C., rate of sexual maturation, oviposition rate, resistance to starvation, and ejection of frass by larvae.

Birch (1944) also found the two "strains" to be intersterile. Some eggs were produced in his interstrain crosses, about 10 percent of which developed to mature embryos, but none hatched. In further work (1946, 1954) he found that the change in size due to change of food was relatively the same in both forms. The small form was relatively common in stored wheat and rare in stored maize. The reverse was true for the large form. In crowded cultures one "strain" always drove the other out, the small one being successful in wheat and the large one in maize.

Kono (1955) studied the rice weevil from several districts in central Nepal. He found the small "strain" predominant in that area. Unlike other populations of the small "strain" which have been reported upon, it was found capable of flight, and observed commonly to infest crops in the field as well as in storage. He made crosses between the Nepalese "strain" and large and small "strains" from Japan and a small "strain" from Australia. The intrastrain crosses were fertile and the interstrain crosses were sterile.

Kiritani (1956) found both forms of *Calandra* to be present in every kind of stored grain. *C. oryzae* (large form) was found to infest grain in the field also, but *C. sasakii* (small form) bred only in grain in storage and did not fly to the field. *C. oryzae* was the more widely distributed species in Japan.

Apparently little attention has been given to the possibility of the occurrence of two species of rice weevils in the United States. Cotton (personal correspondence, 1958) believes that difference in size is a result of food supply and is of

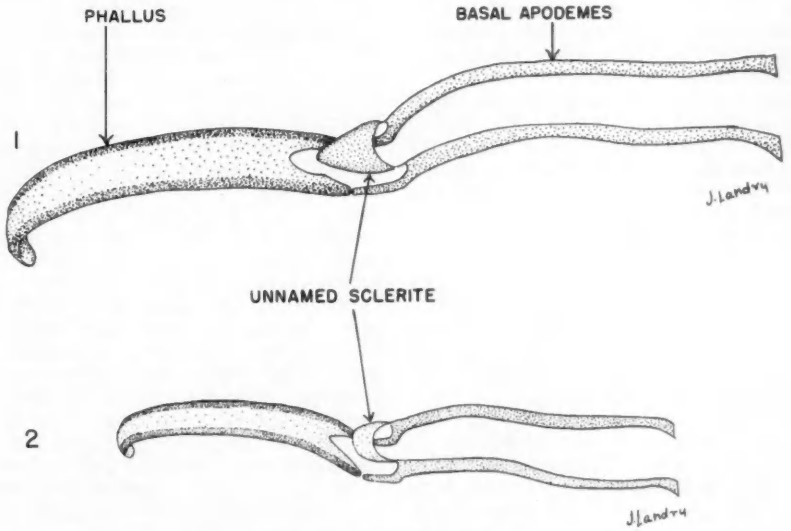


FIG. 1.—Phallus, basal apodemes, and unnamed sclerite, *Sitophilus oryza*, male.
FIG. 2.—Same, *Sitophilus sasakii*, male.

Table 2.—Linear measurements, in millimeters.[a]

Species	Host	Females			Males		
		No. of specimens	Length[b]	Width[c] of thorax	No. of specimens	Length[b]	Width[c] of thorax
S. oryza	Maize	18	3.24±0.25	1.12±0.11	31	3.26±0.27	1.15±0.12
"	Wheat	19	3.09±0.17	1.10±0.08	21	2.97±0.13	1.10±0.06
"	Unpolished rice	23	3.11±0.23	1.09±0.09	28	3.01±0.17	1.07±0.06
S. sasakii	Maize	31	2.85±0.22	0.95±0.09	5	2.72±0.31	0.92±0.09
"	Wheat	26	2.69±0.16	0.89±0.06	14	2.46±0.16	0.83±0.07
"	Unpolished rice	27	2.46±0.18	0.83±0.05	23	2.36±0.11	0.82±0.04

[a]All measurements determined from individuals several days to several weeks of age.
[b]Exclusive of the snout.
[c]Measured at widest point of thorax.

the opinion that only one species is concerned. As noted by Kiritani (1956), Kono (unpublished) reported the occurrence of two species in the United States. Utida (1958) also reported on the distribution of the small species in the United States and Canada.

PROCEDURE

Beginning in 1956, an effort was made to obtain collections of rice weevils from various hosts and localities of the United States. The specimens obtained were classified as to whether they were large or small, based entirely on size.

Differences in size when the two "strains" were reared on the same host and differences in distribution were so pronounced that a study was begun to find morphological characters by which the two could be separated. Later in the study, specimens from all collections were classified relative to newly discovered differences in morphological characters.

Characters such as color, size and sculpturing were found to overlap to a considerable extent. When it was found that these external characters could not be relied upon, the genitalia and associated structures were studied to discover possible differences that would separate the two forms.

Pure cultures of both forms were established. Individual females used to start pure cultures were selected on the basis of size and host, and were confined on uninfested grain in insect-proof breeding jars. After being allowed to oviposit for a period of 1 week, the females were dissected for identification, using the newly found morphological differences between the two.

Breeding experiments were conducted concurrently, using size and host preference to separate the two forms. Unmated individuals were obtained by isolating single infested kernels of corn or wheat in small shell vials. Upon emergence, individuals were sexed and the appropriate crosses were made. Crosses and reciprocal crosses between the large and small forms were made by confining unmated males and females in shell vials on uninfested grain. Each pair was placed in a 2-inch shell vial provided with three kernels of hard red winter wheat. They were maintained in darkness at 80° F. and 65 percent relative humidity. Examinations to establish whether mating had occurred were made between 4 and 16 days after pairing. Mating was considered to have occurred only where sperm could be found in the spermatheca when this organ was dissected under insect Ringers' and examined at 90× magnification.

The specific status of each individual in each cross was vertified at the time of examination for evidence of mating, by use of the morphological character differences between the two species (figs. 1, 2, 3 and 4).

Results of these studies are presented in table 1.

Total length exclusive of the snout, maximum width of thorax, elytral marking, color of dorsum and overall color were studied in specimens of both large and small "strains" established as pure line cultures and reared on maize, wheat and unpolished rice. Results are presented in tables 2 and 3.

Host-preference studies concerned with feeding and reproduction were made. The feeding-preference tests were conducted using different cereal grains in 2-inch glass tubes located symmetrically around a cylinder 3 inches in diameter and 2 inches high. The arrangement of the various grains around the cylinder, inside of which the weevils were introduced, gave each grain equal chance for feeding or oviposition. Readings were made after 48 hours' exposure (table 4). An individual in the act of feeding on a particular grain was considered as the criterion for host feeding preference.

Reproductive potential as influenced by various hosts was determined by using a similar type cage and host arrangement. The grains were exposed for oviposition for 24 hours then removed and maintained at 85° F. and 60 to 70 percent R.H.

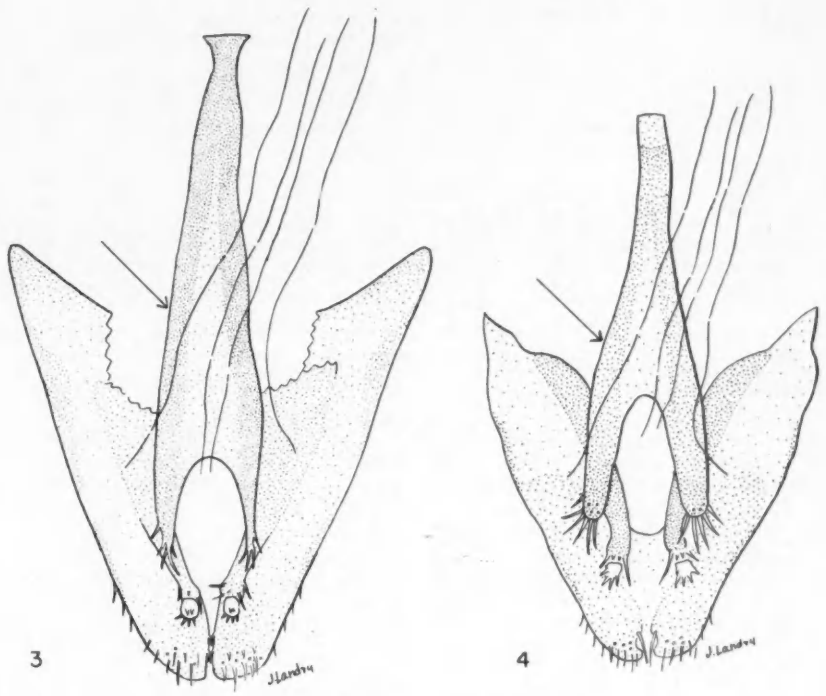


FIG. 3.—Eighth sternum of *Sitophilus oryza*, female.
FIG. 4.—Same, *Sitophilus sasakii*, female.

(table 5). Individuals of the large species used in these tests were selected from a culture which had been reared several generations in corn. The small species came from a culture reared an equal number of generations in wheat.

The effect of crowding was studied when the two forms were confined on various hosts. This test was conducted in ½-pint fiber cartons, three-fourths filled with grain and stored at 85° F. and 60 to 70 percent R.H. The food supply was changed when 75 percent of the kernels of either rice or wheat contained one emergence hole each or when 75 percent of the maize kernels contained two or more emergence holes (table 6).

DISCUSSION OF RESULTS

Examination of rice weevils found in grain samples from several states of the United States showed that while the small form was present throughout the South, the large form occurred far more commonly in this area. Only the small one was found in the samples of grain examined from the more northerly states. The small form was found in grain from Arkansas, California, Florida, Kansas, Louisiana, Mississippi, North Carolina, Oklahoma and Texas. The large form was recorded from Arkansas, Alabama, Florida, Louisiana, Mississippi, South Carolina, North Carolina and Georgia. The absence of either of the forms from any state should not be interpreted to mean that it does not occur there, since only a few samples were examined from most states. One infestation of the small form each in stored and in standing maize has been found to date. These infestations were found in northeast Louisiana on the same plantation. Wheat had been grown on this farm several seasons previously, and was found heavily damaged in storage by the small rice weevil.

Studies by Birch (1944) and Kiritani (1956) show the small form is favored by higher temperatures. It would normally be expected therefore that the small "strain" should be the dominant form in the southern part of the United States and the large one dominant in the more northerly latitudes. This, however, is not the case. In way of explanation of this reversal in expected distribution of the forms, it appears likely that the preferred host is of more importance than the temperature difference between the areas. Previous to the second World War, wheat grown as a grain crop or grain sorghum was practically unknown in the south except in Texas. Maize represented the only stored grain in the south until this time, and the small form does not favor this grain for feeding or for oviposition.

Table 3.—Effect of host on color of the two species.

Species	Host	Elytral spotting			Color of dorsum			Body color		
		Distinct	Vague	Merged	Dark	Medium	Light	Dark	Medium	Light
		%	%	%	%	%	%	%	%	%
S. oryza	Maize[a]	30.7	19.6	49.6	36.0	54.7	9.2	12.7	36.5	50.8
"	Wheat[b]	0.0	57.0	42.9	0.0	87.6	12.4	0.0	49.9	50.1
"	Rice[c]	84.9	6.9	8.2	67.5	28.6	3.9	33.8	54.5	11.7
S. sasakii	Maize	32.9	27.7	39.4	4.8	47.4	47.7	1.6	46.1	52.3
"	Wheat	0.0	1.9	98.1	0.0	5.8	94.2	0.0	0.0	100.0
"	Rice	0.0	7.7	92.3	0.0	0.0	100.0	0.0	0.0	100.0

[a]Louisiana 521.
[b]An unknown variety of hard winter subclass of the class hard red winter.
[c]Zenith (unpolished).

On the other hand, maize is a preferred host of the large form. The more northerly states produce and store much wheat, a preferred host of the small form.

Difference in the shape of the eighth sternum of the female and in the shape of the sclerite at the juncture of the basal apodemes and the phallus of the aedeagus of the male were found to afford reliable characters for separating the two forms. Differences in these structures are illustrated in figures 1, 2, 3, and 4.

Table 4.—Feeding preferences of the two species (seven replicates per host).

Host	Percent individuals feeding after 48 hours		Grain moisture %
	S. oryza[a]	*S. sasakii*[a]	
Maize	10.4	2.2	13.76
Wheat	6.7	18.6	12.60
Unpolished rice	40.0	28.2	13.50
Sorghum[b]	32.8	35.0	15.82

[a]Source of *oryza*, maize; source of *sasakii*, wheat.
[b]Martin combine milo.

Data obtained from several sources (Richards 1944, Birch 1944, 1946 and 1954, and Kono 1955), as well as results of this study, show that the two forms of *Silophilus* (=*Calandra*), apparently cosmopolitan in distribution and variable in size and color, are deserving of specific status. Richards (1944) was unwilling to accept results of his experiments showing intersterility between his large and small forms as a basis for establishing specific status of the two as species, since no nonoverlapping morphological differences were found.

Birch (1944, 1952) showed intersterility between the two forms and concluded that sibling species were involved.

Kono (1955) demonstrated intersterility in a cross of a Nepal small form with the large form from Japan. Crosses between this form and small forms from both Japan and Australia were fertile.

Data presented in table 1 show intersterility in crosses between large and small species from the United States. Unlike results reported by Richards (1944) and Birch (1944), mating did not occur between these two forms. Copulation was observed in virtually 100 percent of the cases when large × large or small × small crosses were made. Examination of the spermatheca from females in these crosses showed an abundance of motile sperm. Where large × small or the reciprocal cross was attempted, copulation was never observed and examination of the spermatheca showed the absence of sperm.

The large species showed a definite feeding preference for unpolished rice, grain sorghum, maize (corn), and wheat in the order named; the small species chose grain sorghum, unpolished rice, wheat, and maize (table 4).

Completion of development under comparable conditions was indicated by adult emergence. The greatest number of the large species emerged from grain sorghum, followed by unpolished rice, wheat, rough rice, and maize in the order named; the greatest number of the small species also emerged from grain sorghum, followed by wheat, unpolished rice, rough rice, and maize (table 5).

A study to determine the effect of crowding (table 6) by one species on the other, when the two were confined in a common cage on a common host, showed that the large species was dominant when the host was maize or unpolished rice. When the host was wheat, the small species became dominant. These results with maize and wheat are in agreement with those reported by Birch (1954). In rough rice the trend was for the small species to become dominant. The smaller species is apparently capable of breeding in and emerging from kernels of rough rice, in

which narrow openings between the palea and lemma probably form a physical barrier to the large species.

Studies of the genitalia and associated structures revealed morphological differences for separation of the two forms. The sclerite at the juncture of the phallus and the basal apodemes is a broadly triangular structure in the large species and is a narrow crescent-shaped structure in the small species, (figs. 1 and 2). The eighth sternum in the female of both species is reduced to a small Y-shaped structure, (figs. 3 and 4). In the large species, the fork of the Y is relatively shallow and the lobes are acutely pointed. The distal end of the sternum is distinctly knobbed. In the small species, the fork of the Y is relatively deep and the lobes are broadly rounded at their apices. The distal end of the sternum is not knobbed; however a somewhat swollen appearance has been observed near the distal end in some individuals.

The average size of individuals shows considerable difference between the two species (table 2). However, overlaps occur in all the linear measurements. This prevents 100 percent accuracy in species determination based on size alone. The average size of individuals of both species is influenced by the host from which they are bred. Maize (corn) produced the largest individuals (table 2). There was very little difference in size as influenced by rice or wheat. Distinctness of the elytral spots (actually a contrast as determined by the degree and extent of pigmentation in the elytra), the color of the dorsum, and the general body color are influenced by the host (table 3). Rice produced the highest percent of individuals with distinct elytral spots in the large species. Individuals of the large species reared from wheat did not show these distinct spots. Maize (corn) produced less than one-half as many distinctly spotted individuals as did rice. The same trend held true for the color of the dorsum and the general body color. In contrast, only maize (corn) produced individuals of the small species in which elytral spots were classed as distinct. These represented approximately 30 percent of the individuals. Rice and wheat produced individuals of the small species which were devoid of spots (superficially). Individuals of the small species which developed from maize (corn) tended to have a darker dorsum than those which developed from other hosts. The same trend was true for the general body color. Individuals of the small species reared from rice and wheat were light tan in color. No dark specimens were found.

Table 5.—Reproductive potential as influenced by various hosts.[a]

Host	Average number progeny per replicate after 45 days (complete emergence)		Grain moisture[c] %
	S. oryza	*S. sasakii*	
Maize	3.0	1.0	13.76
Wheat	18.0	42.0	12.60
Rough rice[b]	6.0	4.0	12.13
Unpolished rice	86.0	10.0	13.50
Sorghum	87.5	44.0	15.82
Oats	0.0	0.0	11.85

[a]Twenty females and five males used per replicate; four replicates per host. Test conducted at 85° F. and 60 to 70 percent R.H. Source of *oryza*, maize; of *sasakii*, wheat.
[b]Zenith.
[c]At beginning of test.

Differences in average size and color, although useful, proved too variable to be relied upon completely for separating the two species. Differences in sculpturing of the pronotum as described by Kono (1955) have proved reliable for specimens studied from the United States, England, Japan, and Trinidad.

Since the Linnaean specimens apparently have been lost, it is impossible to be certain of the name

Table 6.—Effect of crowding when both species are confined together.[a]

Host	Grain moisture[b] %	Avg. no. progeny per replicate after 7 months	Species ratios			
			Generations 1, 2, 3		Generations 4, 5, 6	
			S. oryza	*S. sasakii*	*S. oryza*	*S. sasakii*
Unpolished rice	13.50	1,031	72.3	27.7	93	7
Wheat	12.60	1,548	52.0	48.0	18	82
Rough rice	12.13	114	78.0	22.0	62	38
Maize	13.76	282	92.0	8.0	97	3

[a]Five females and three males used per replicate; four replicates per host. Test conducted at 80° F. and 60 to 70 percent R.H. Source of *oryza*, maize; of *sasakii*, wheat.
[b]At beginning of test.

which is correctly applicable to each of these species. European workers in general have been of the opinion that *S. oryza* (L.) applied to the small species. Apparently this has been the more common of the two species in Europe, since both Motschulsky (1855) and Zacher (1922) described the large species as a variety.

In contrast to these views, Japanese workers have considered *S. oryza* (L.) applicable to the large species. Takahashi (1928) described the small species as *Calandra* (=*Sitophilus*) *sasakii*.

Since it is apparent that two species are involved, it is necessary that the nomenclature be clarified.

Linnaeus' description of *oryza* contained the following three significant points:

1. Color all black or pitch black.
2. Color of dorsum beneath the elytra pitch black.
3. Two iron-colored stains present on the elytra, one at the base and one at the apex.

The size, which he gave as that of a grain of rice, is meaningless at this time. Even if a more precise measurement had been given, it is now known that there is a considerable amount of overlap between species. The fact that it was described from rice gives no indication which species was involved, since it is known that rice is at least as favorable a host for the large species as for the small one.

Although black specimens with pitch-black dorsum and distinct elytral spots occasionally have been identified as the small species, they occur rarely.

After considering all these factors, we conclude that the name *Sitophilus oryza* (L.) is applicable to the large species, and *Sitophilus sasakii* (Takahashi) to the small species. The common name "lesser rice weevil" is suggested as appropriate for *S. sasakii*.

Specimens considered typical of the two species have been deposited in the U. S. National Museum.

SYNONYMY OF *S. oryza* (L.)

Curculio oryza Linnaeus 1763: 395.
Calendra oryzae (L.) de Clairville and Schellenberg 1798: 62.
Sitophilus oryzae (L.) Schönherr 1838: 967.
Sitophilus Zea-mais Motschulsky 1855: 77–78.
Calandra oryzae var. *platensis* Zacher 1922: 55–56.

The genus *Calendra* was erected by de Clairville and Schellenberg in 1798 to include *abbreviata* Fab., *granarius* L., and *oryzae* L. The name was misspelled *Calandra*, and has been used in this form for *oryzae* L. by many authors. In 1838 Schönherr restricted *Calendra* to the bill bugs, with *abbreviata* Fab. as type, and erected *Sitophilus* for *oryzae* L. (type) and *granarius* L. (Hemming 1957).

The Secretary of the International Commission on Zoological Nomenclature has recommended to the Commission that *Calandra* be placed on the Official List of Rejected Generic Names, and that *Sitophilus* be placed on the Official List of Accepted Generic Names. He also is placing before the Commission a recommendation to validate the emendation to *oryzae* of the specific name *oryza* Linnaeus 1763, published in the combination *Curculio oryza* (see Hemming 1957).

SYNONYMY OF *S. sasakii* (TAK.), NEW COMBINATION

Calandra oryzae var. *minor* Sasaki 1899, p. ? (fide Kiritani 1956).
Calandra oryzae (L.) Zacher 1922: 55–56. Schmidt 1925: 233–5.
Calandra sasakii Takahashi 1928: 164, and 1931: 83.

The varietal name *minor* has no nomenclatorial standing. Zacher (1922) and Schmidt (1925) used *oryzae* L. for the small species, believing that Linnaeus' specimens were of this type. Takahashi was the first reviser, but used the wrong generic name.

ACKNOWLEDGMENTS

The authors are indebted to the following individuals who kindly assisted in this study: to the Rev. Father Daniel F. Becnel, Pastor, St. Aloysius Catholic Church, Baton Rouge, Louisiana for a translation of the Linnaean description of *Curculio oryza*; to G. A. Bieberdorf, Oklahoma, B. W. Clements, Georgia; W. G. Eden, Alabama; C. F. Garner, Texas; R. Hutchins and A. Hamner, Mississippi; Robert Jones and W. J. Wiser, Florida; Walter Kulash and W. V. Campbell, North Carolina; Charles Lincoln, Arkansas; S. Marcovitch, Tennessee; W. A. Price, Kentucky; J. K. Reed, South Carolina; R. Strong, California; and Don Wilbur, Kansas who supplied insect specimens and insect-infested grains from their respective states; to M. H. Breese, Imperial College of Agriculture, Trinidad, B.W.I., O. W. Richards, Imperial College, Kensington, S. W., and Toyoaki Harada, The Food Research Institute, Ministry of Agriculture and Forestry, Tokyo, who kindly sent specimens from their countries for study; to Mr. Shizuo Kato, Entomologist, The National Institute of Agricultural Services, Tokyo, and Prof. Keizi Kiritani, Entomologist, Kyoto University, Kyoto, Japan for supplying literature and translations of the Japanese work relative to rice weevil studies in Japan; to Miss J. Landry, Louisiana State University, for the illustrations used in this study; to R. B. Selander, Illinois State Natural History Survey, for identification of the morphological structures used in the taxonomic study of the two species; and to Mr. J. W. Ingram, United States Department of Agriculture, for assistance in procuring valuable literature from Japan.

The authors wish to express special appreciation to the following persons who criticized the manuscript and made many helpful suggestions: Pauline Davy, Robert Howe, J. W. Ingram, R. H. Painter, O. W. Richards, Ed. Soderstrom, and D. A. Wilbur.

REFERENCES CITED

Birch, L. C. 1944. Two strains of *Calandra oryzae* (L.) (Coleoptera). Australian Jour. Exptl. Biol. and Med. Sci. 22: 271–5.

1946. The influence of food on the size of two strains of *Calandra oryzae* L. Ibid. 24: 123–5.

1954. Experiments on the relative abundance of two sibling species. Australian Jour. Zool. 2(1): 66–74.

de Clairville, J. P., and **J. R. Schellenberg.** 1798. Entomologie Helvétique. Helvetische Entomologie. Bd. 1. Zürich. 149 pp. (Bilingual; German version by Schellenberg, French translation by de Clairville.)

Hemming, Francis. 1957. The *Calandra/Calendra* problem (Class Insecta, Order Coleoptera). Bull. Zool. Nomencl. 16(1): 5–47.

Kiritani, K. 1956. On the local distribution of two allied species of the rice weevil, *Calandra oryzae* and *C. sasakii*. Japanese Jour. Appl. Zool. 21(2): 74–77.

Kono, T. 1955. Rice weevil. (Scientific Results of the Japanese Expeditions to Nepal Himalaya 1952–53). Fauna and Flora of Nepal Himalaya 1: 383–5.

Linnaeus, C. 1749–69. Amoenitates Academicae seu Dissertationes Physicae, Medicae, etc. 7 vols. Lugduni Batavorum. (Vol. 6, 1763, p. 395.)

Motschulsky, V. 1853–62. Études entomologiques. 11 vols. (Vol. 4, 1855, Helsingfors, pp. 77–78.)

Richards, O. W. 1944. Two strains of the rice weevil, *Calandra oryzae* (L.). (Coleopt., Curculionidae). Trans. Roy. Ent. Soc. London 94: 197–200.

Sasaki, C. 1899. Insects Injurious to Agricultural Crops. Tokyo. (Not seen by the authors; cited after Kiritani 1956.)

Schmidt, M. 1925. Die morphologische Unterschiede von *Calandra oryzae* (L.) und *Calandra zea-mais* Motsch. (*platensis* Zacher). Arb. biol. Reichsanst. f. Land- u. Forstwirtschaft 12: 233–5.

Schönherr, C. J. 1837–8. Synonymia Insectorum, etc. 1. Käfer. 4. Theil. Curculionides. Genera et species Curculionidum cum synonymia hujus familiae. Band 4. Paris. (Part 1, 1837, pp. 1–600; Part 2, 1838, pp. 601–1094.)

Takahashi, S. 1928. Insects injurious to field crops. Meibundo 1928: 164.

1931. Insect pests of grain and their control measures. Ibid. 1931: 83.

Utida, S. 1958. Distribution of the small rice weevil in the United States. Jour. Econ. Ent. 51(6): 913.

Zacher, F. 1922. Eingeschleppte Vorratsschädlinge. Verh. deutsch. Ges. angew. Ent., E. V. dritten Mitgliederversamml. Eisenach 28–30 Sept. 1921, pp. 55–56.

Zumpt, F. 1935. Revision der europäischen *Calandra*-Arten. Curculioniden-Studien XII. En Blättert. 31(2): 55–59.

STUDIES ON THE HEXAPOD NERVOUS SYSTEM. I. THE PERIPHERAL DISTRIBUTION OF THE THORACIC NERVES OF THE ADULT COCKROACH, PERIPLANETA AMERICANA[1]

RUDOLPH L. PIPA[2] AND EDWIN F. COOK[3]

ABSTRACT

Eight pairs of nerves emanate from each of the three thoracic ganglia of the adult American cockroach. An additional chiasmic nerve, probably proprioceptive in function, is present in the prothorax. The interganglionic connective is designated as nerve 1. Nerve 2A supplies the intersegmental muscles and others which, collectively, probably play an important role in the maintenance of posture. Nerve 2B of the meso- and metathorax is primarily sensory to the spiracular region, tegula, wings, and axillary region. Nerve 2C supplies the dorsal longitudinal and oblique muscles. Nerve 3A supplies coxal adductors and promotors, while 3B comprises the major sensory supply of the coxa. Nerve 4 supplies the main depressor of the leg, certain coxal remotors, and muscles which probably act as adductors and rotators. In the coxa nerve 5 is sensory to the coxal wall and meron, motor to the coxal branches of the main leg depressor. Nerve 6A supplies the coxal remotors; 6B the major levators of the leg, as well as muscles which probably function as coxal rotators or rotator-adductors. Nerve 7 provides the sensory supply of the basisternal and furcasternal setae. Nerve 8 supplies the spiracular closing muscle. The metathoracic and first abdominal ganglia are fused. The two nerves emanating from the first abdominal ganglion are characterized. Difficulties likely to be encountered in using nerve distribution to establish muscle homologies are discussed.

A study of nerve distribution may be approached with at least two different goals in mind. Increasing attention is being paid to the hexapod nervous system by insect morphologists in attempts to establish muscle homologies and, in turn, shed light on the course of phylogenetic development. It is also indisputable that a knowledge of anatomy is fundamental to physiological investigations. This is particularly true of neuroanatomy. This paper is primarily an attempt in the latter direction.

When one considers the importance of the American cockroach as an experimental insect in investigations on sensory and neuromuscular mechanisms, it is rather surprising to note that little is actually known about the gross anatomy of its thoracic nervous system. Other than the excellent papers by Nijenhuis and Dresden (1952, 1955a), the only strictly anatomical work which might be at all useful in this respect is that by

[1]Paper No. 4080, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. Accepted for publication March 2, 1959.

[2]Current address: Department of Anatomy, Albert Einstein College of Medicine, New York 61, New York.

[3]Department of Entomology and Economic Zoology, University of Minnesota, St. Paul 1.

Matsuda (1956). The latter is limited to a treatment of the distribution of the motor nerves in the thorax of the German roach, *Blatella germanica* (L.). Its applicability, therefore, would depend upon the degree of similarity between the nervous systems of the two species. The papers by Pringle (1939) and Case (1957) could conceivably be of some value also, though their approach is essentially physiological.

This study was undertaken because a knowledge of the peripheral distribution of the thoracic nerves was considered prerequisite to an investigation of the internal organization of the thoracic ganglia. Such an investigation is now in progress at this laboratory. Though Nijenhuis and Dresden (1952, 1955a) treat the distribution of the mesothoracic nerves in detail, they emphasized those involved primarily with the sensory and motor mechanisms of the legs. The distribution pattern of the prothoracic and metathoracic nerves has not been mapped up to this time. Assuredly, homologous nerves are to be expected in the three metameres, but the facts that the prothorax is not directly involved with the motor mechanism of flight, and that the metathoracic ganglion is fused with the first abdominal ganglion, increase the probability that differences do exist. Variations in the size and distribution of the muscle components of the three regions might also be expected to influence the pattern of nerve ramification.

MATERIAL AND METHODS

Adult male roaches were usually selected because they apparently contain less stored fat than females do. Stored fat was also reduced by starving for a month or so before dissection. Killing and fixation were achieved by injecting 95 percent ethanol into the haemocoele. Immediately after being injected, each roach was placed in either a prone or supine position at the bottom of a petri dish containing a mixture of powdered charcoal in melted beeswax and paraffin. This mixture was used when just above its melting point. After orienting the roach, the mixture was rapidly solidified in cold water, and the dish was partially filled with more 95 percent ethanol, and covered. Such preparations were satisfactorily maintained for weeks by periodically refilling with ethanol. Nerves were followed to the regions which they supply by carefully teasing with sharpened jeweler's forceps under a stereoscopic microscope. Differentiation was enhanced by applying aceto-carmine or Van Giesen's stain with a finely drawn medicine dropper.

Fortunately, the thoracic muscles have been treated by Carbonell (1947). The numbers which he applied to these muscles have been indicated at the ends of the nerves which supply them (figs. 1 through 4). Several muscles which were overlooked by Carbonell, as well as sensory fields, are indicated by abbreviations which will be explained in the text. An effort will be made to discuss all muscles in a manner which will include mentioning their points of attachment as well as names and numbers. Carbonell's characterizations of the muscles will be followed closely throughout.

The designation of nerves presents a particular problem. In general, the system employed by Nijenhuis and Dresden (1952, 1955a) will be adopted here despite the fact that homologous rami do not invariably arise from the same points in different individuals, nor from the same points in different segments of the same individual. Nerve rami which are obviously homologous to those indicated in the mesothorax by these workers will be given the designations used by them, even though this may appear illogical with respect to the other rami of the particular nerve under consideration. This is done to preserve homogeneity. Where homologies are not obvious, a different system will be used. Due to variations between individuals, it must not be expected that the accompanying figures depict a pattern which will be found in every case. Some of the deviations which have been encountered will be mentioned. The figures presented here, however, do typify the pattern observed most frequently, and it is hoped that they will serve as a general guide. It will be noted that the distribution of the leg nerves was not pursued farther than the coxae. The trochanteral and femoral nerves of the mesothorax are treated by Nijenhuis and Dresden.

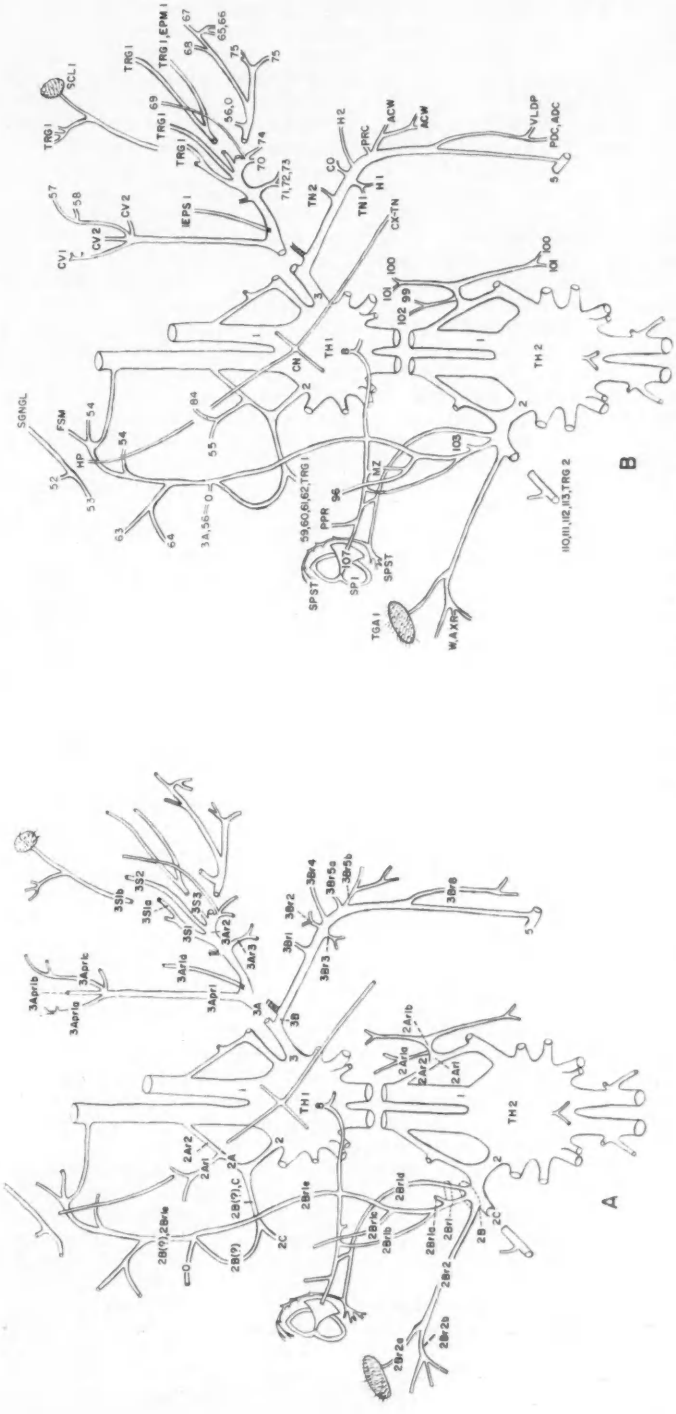
NERVES OF THE PROTHORACIC GANGLION

The prothoracic ganglion is the smallest ganglion of the three thoracic metameres. This might be partially explainable in terms of the relatively reduced muscular mass which it innervates. At least, it is recognized that the extent of the peripheral field influences the size of the nerve center which supplies it (Power 1943, 1946).

Two of the neck muscles are clearly innervated by a nerve branch (SGNGL, fig. 1B) from the suboesophageal ganglion. These include the first cervical muscle of the head (52) which arises from the dorsal cervical sclerite, and the protergal muscle of the head (53) which arises from the midprotergum. Both are inserted laterally on the postoccipital ridge of the head.

There are eight pairs of nerves which definitely emanate from the prothoracic ganglion. The ninth, which will be termed the chiasmic nerve (CN, fig. 1B) very likely originates here as well. Nerve 1 designates the interganglionic connective which joins the prothoracic ganglion to the suboesophageal ganglion of the head.

Nerve 2: This nerve (fig. 1A) branches to form the intercalary nerve (2A) and nerve 2B(?),C. The interrogation mark indicates that it is



EXPLANATION OF FIGURE 1

A. Dorsal aspect of pro- and mesothoracic ganglia with peripheral rami of nerves 2 and 3 designated.
B. Same as A, but with innervation fields designated.

questionable whether 2B is homologous to 2B of the meso- or metathorax. Nerve 2A gives rise to two rami. The first, 2Ar1, carries fibers which innervate the longitudinal ventral muscle of the head and prothorax. This muscle (55, fig. 1B) inserts on the tentorial bridge of the head. The prosternal muscle of the cervical sclerite (84) which goes to the second cervical sclerite is also innervated by fibers from 2Ar1. Muscles 55 and 84 arise on the sternal arm. Nerve 2Ar2 fuses with the interganglionic connective.

Nerve 2B(?),C branches to form 2B(?) and 2C. Nerve 2B(?) fuses with 2Br1e from the mesothoracic ganglion. The pattern of fiber distribution resulting from this fusion (2B(?), 2Br1e, fig. 1A) requires histological clarification. Tentatively, we may say that certain of the fibers resulting from this fusion give rise to nerve O, a very fine nerve which, in turn, fuses with a branch from nerve 3A (56, O, fig. 1B). A part of this second fusion innervates the episternal muscle of the head (56) which arises from the episternum and inserts dorsally on the postoccipital ridge of the head.

The remaining branches resulting from the fusion of 2B(?) and 2Br1e innervate the first and second protergal muscles of the first cervical sclerite (63 and 64), the second cervical muscle of the head (54), and the foregut suspensor muscles (FSM) (fig. 1B). Muscles 63 and 64 arise on the protergum and terminate on the first ventral cervical sclerite. Muscle 54 arises from the cervical integument and inserts on the tentorial bridge of the head. The foregut suspensor muscles pass from the walls of the foregut to the lateral walls of the occipital foramen. An interesting feature is the fusion of a branch from 2B(?),2Br1e with the interganglionic connective.

Nerve 2C of the prothorax is entirely homologous to its counterparts in the meso- and metathorax. Branches from 2C innervate the prothoracic longitudinal dorsal muscle (59), the oblique dorsal muscles (60, 61), and the transverse dorsal muscle (62). It also plays a role in the sensory innervation of the protergum (TRG 1). Muscle 59 extends from the middle of the first phragma anteriorly to the neck integument. Muscles 60 and 61 arise from the midpronotum and terminate on a small sclerite attached to the lateral part of the first phragma, very close to the base of the fore wing. Muscle 62 passes from the middle part of the phragma to the same terminus as 60 and 61.

Chiasmic nerve: This name was suggested by the definite X-shape of the component rami. The chiasmic nerve (CN, fig. 1B) appears to arise from the middorsal anterior aspect of the prothoracic ganglion. It is normally in close association with the external ganglionic connective tissue and this obscures the details of its origin.

Two fine rami course anteriorly and may be closely applied to the second protergal muscle (64) on either side of the body. It is uncertain whether muscle 64 is actually innvervated. Each ramus may be so closely associated with the anteriormost portion of nerve 2B(?),2Br1e that it appears to be a branch which issues from it. A major segment of each anterior ramus of the chiasmic nerve supplies a hair-plate (HP, fig. 1B) located at the junction of the head and the first cervical plate. Two rami also pass posterolaterally. Each was traced to the cuticle where the first and second trochantin join the coxa (CX–TN, fig. 1B).

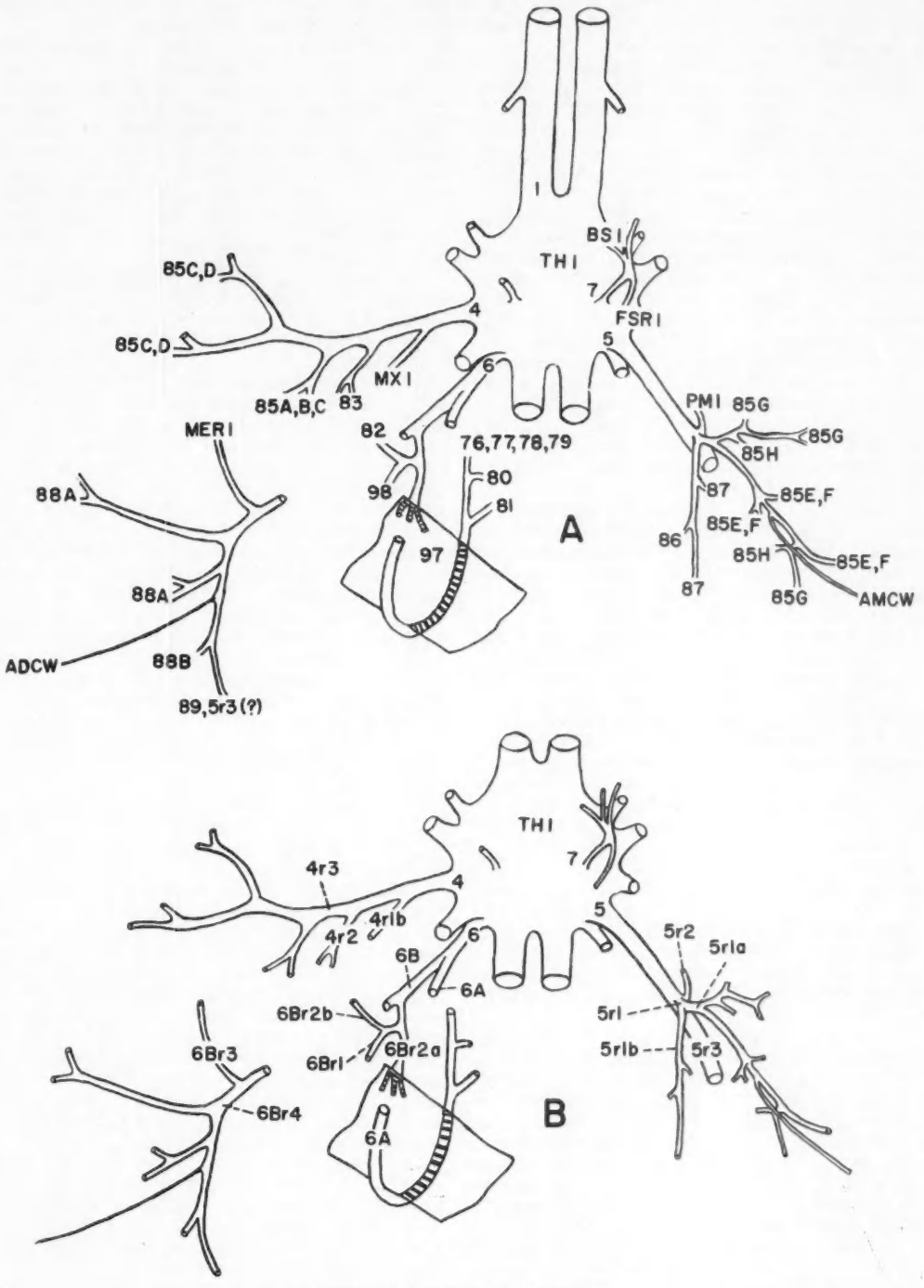
Nerve 3A: The first branch of this nerve is designated 3Apr1 (fig. 1A) because it does not appear to be homologous to 3Ar1 of the meso- or metathorax. Nerve 3Apr1a constitutes the major sensory supply of the first cervical plate (CV 1); 3Apr1b that of the second (CV 2). Nerve 3Apr1c supplies the cephalic muscles of the cervical sclerites (57, 58). These arise on the dorsal postoccipital ridge. Muscle 57 terminates on the first ventral cervical plate; 58 on the second.

Nerve 3Ar1a is homologous to its counterpart in the meso- and metathorax. It may arise from several points on 3A, or even from 3B in different roaches. Other points of origin which have been seen are depicted by broken patterns in figure 1. This is an example of the variation which makes nomenclature difficult. This nerve constitutes the major sensory supply of the first episternum of the prothorax (1EPS 1, fig. 1B). The prothoracic homolog of nerve 3Ar1b of the other thoracic ganglia could not be established with certainty.

Nerve 3Ar3 supplies the second (71), third (72), and fourth (73) tergal muscles of the trochantin. The first tergal muscle of the trochantin (70) is innervated by a separate branch from 3Ar2. All of these muscles arise from the tergum and insert on the first plate of the trochantin. Another branch from 3Ar2 innervates the tergal promotor of the coxa (74). This muscle arises from the tergum and inserts on a small sclerite located near the coxoepimeral articulation.

A very fine nerve arises from the junction of the nerves supplying 70 and 74. This ramus innervates the protergal muscle of the neck (69) which arises from the anterior protergum and terminates on a fold of the ventral integument of the neck.

On the basis of innervation pattern alone, it is suggested that the sternopleural promotor of the coxa (75) is homologous to the sternopleural promotor of the mesothorax (127) and to the second episternal promotor of the metathoracic coxa (168, fig. 3B). Muscle 75 originates on the episternum and under side of the pleural ridge. It inserts on the same small sclerite as 74. Muscle 127 and 168 have an origin similar to that of 75, and each inserts on a small plate near the coxopleural articulation. This small plate is most



EXPLANATION OF FIGURE 2

A. Ventral aspect of prothoracic ganglion with innervation fields of nerves 4, 5, 6, and 7 designated.
B. Same as A, but with peripheral rami designated.

likely homologous to the small sclerite which serves as the insertion for muscle 75.

Nerves 3S1, 3S2, and 3S3 are purely sensory nerves which do not have obvious counterparts in the other thoracic segments. Nerve 3S1a is sensory to the midanterior protergum (TRG 1, fig. 1B), especially near the junction of the latter with the dorsal cervical sclerite. Nerve 3S1b provides the sensory supply of the anterolateral protergum and a small sclerite (SCL 1) which is replete with numerous setae. This sclerite is located just anterior to the pleural ridge and slightly ventrad to the anterolateral protergum. Nerve 3S2 also supplies the protergum, apparently in the vicinity of the attachments of the first and second protergal muscles of the pleural arm (65, 66). Nerve 3S3 is sensory to the anterolateral protergum. A branch of 3S3 innervates the protergal region anterior to the epimeron (TRG 1, EPM 1) as well. It is very probable that this branch is sensory to the epimeron, too.

Another nerve which arises from 3Ar2 fuses with nerve O from 2B(?),2Br1e. As mentioned previously under the discussion of the branches from nerve 2, this fusion supplies muscle 56. A branch from 3Ar2 also gives rise to a number of rami which supply the first (65), second (66), third (67), and fourth (68) protergal muscles of the pleural arm. All of these muscles pass from the protergum to various parts of the pleural arm. The homologs of muscles 56, and 65 through 69, were not obvious. An interesting speculation is that certain of the muscles 65, 66, 67, 68, and 69 are homologous to the tergopleural muscle (114, 157), the pleuroalar muscle (115, 158), and the tergopleural muscle (116, 159) of the wing-bearing segments. This is suggested by the absence in the prothorax of other muscles which might be homologs of these; a similarity in points of attachment with differences which could be explained by assuming that migrations had occurred; and the absence of any other nerve in the prothorax which could be homologized with 3Ar1b of the meso- or metathorax. An obvious difference between 3Ar1b of the meso- and metathorax and this nerve is the failure of this nerve to fuse with a branch of 6A (i.e., see nerve 6Ar4, figs. 3C, D).

Nerve 3B: The nerve indicated by the broken line issuing from 3B in figure 1A represents one point of origin of 3Ar1a which was observed a number of times. As in the pterothorax, nerve 3Br1 constitutes the major sensory supply of the second trochantin. According to the histological investigation of Nijenhuis and Dresden (1952), nerve 3Br2 supplies a coxotrochantinal chordotonal organ. An apparent prothoracic counterpart to 3Br2 is shown in figure 1A. The presence of a chordotonal organ (CO, fig. 1B) is inferred solely on the assumption that this nerve is homologous to nerve 3Br2 of Nijenhuis and Dresden. No histological examination of the innervated field was undertaken. This nerve can be followed to the region of the coxotrochantinal articulation, however.

Nerve 3Br3 branches to supply the first trochantin (TN 1) and a coxal hair-plate (H1) at the inner junction of the coxa with the pleuron. Nerve 3Br4 supplies the outer coxal hair-plate (H2). Nerve 3Br5a supplies a proximal coxal chordotonal organ in the mesothorax according to Nijenhuis and Dresden (1952). It is assumed that its prothoracic counterpart has a similar function (see PRC, fig. 1B).

The setae of the anterior (ventral) coxal wall are supplied by numerous branches from 3Br5b. The manner of branching of this nerve in the prothorax differs from that in the metathorax as can be seen by comparing figure 1A with figure 3A. The counterpart of nerve 3Br8 of the meso- and metathoracic ganglia was also found in the prothorax. One distal branch of this nerve supplies the ventrolateral coxal projection (VLDP, fig. 1B); the other posterior (dorsal) and anterior (ventral) distal coxa (PDC, ADC) where, according to Nijenhuis and Dresden (1952), chordotonal organs are located.

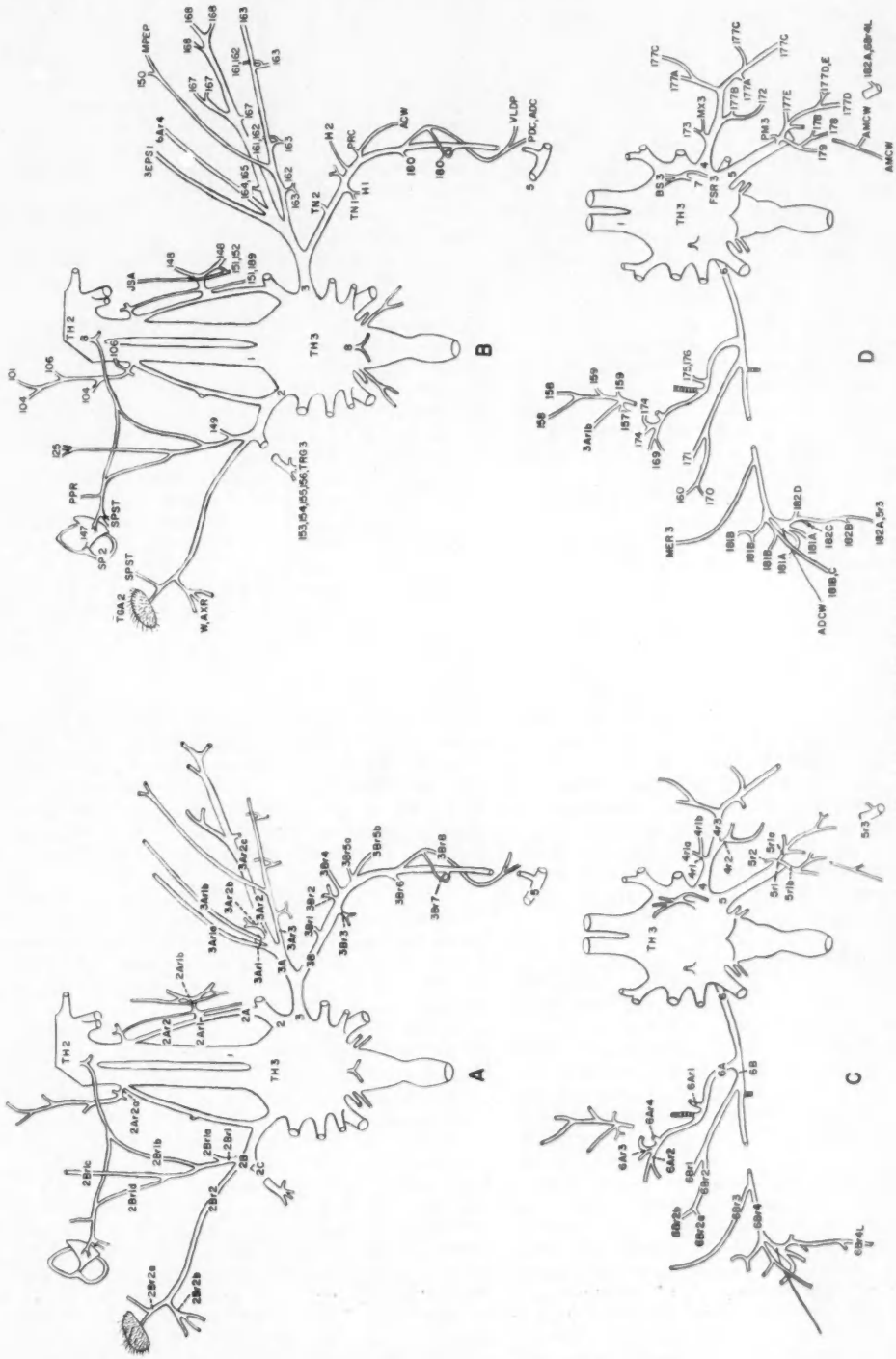
Nerve 3B in the prothoracic coxa differs from its counterparts in the meso- and metathorax in lacking motor rami. This is not surprising, since a prothoracic counterpart of the anterior coxal levators of the meso- and metathorax (138, 180) is absent, and since this muscle is the only one supplied by a branch of 3B in the coxa. As is the case in the other two thoracic segments, a branch of 3B fuses with nerve 5 in the trochanter.

Nerve 4: Branches of this nerve were traced exculsively to muscles. From external appearances, then, one would be led to the conclusion that this nerve serves a purely motor function.

The most proximal branch of nerve 4 (4r1b, fig. 2B) supplies a muscle which has escaped the attention of Carbonell and others. This muscle (MX 1, fig. 2A) is very thin and extends from the antero-lateral aspect of the furcasternum to the coxal rim where the second trochantin articulates. Meso- and metathoracic (MX 3, fig. 3D) counterparts of this muscle have been found.

Nerve 4r2 supplies the sternal muscle of the coxa (83, fig. 2A). This muscle arises on the sternal arm and extends to the basicosta of the coxa. On the basis of innervation 83 would be considered homologous to the sternal remotors of the mesothorax (132) and metathorax (172). It would not be considered homologous to the sternal muscles of these segments (133, 170, or 171), for the latter two are innervated by fibers from nerve 6Br2 and 6Br1 (see figs. 3C, D). This is an example of the value of a knowledge of nerve distribution for a proper designation of muscles, such a method of designation being based on the establishment of homologies.

Nerve 4r3 sends numerous branches to the tergal (85A, B) and pleural (85C, D) branches of



EXPLANATION OF FIGURE 3

A. Dorsal aspect of posterior mesothoracic and metathoracic ganglia. Peripheral rami of nerves 2 and 3 are designated.
B. Same as A, but with innervation fields designated.
C. Ventral aspect of metathoracic ganglion. Peripheral rami of nerves 4, 5, and 6 designated.
D. Same as C, but with innervation fields designated.

the main depressor of the leg. Branches 85A and B originate on the tergum; 85C and D on the pleural arm and ridge. All four branches insert on a broad apodemal tendon which arises from the proximal angle of the trochanter.

Nerve 5: This is a very important sensory nerve of the leg. The mesothoracic trochanteral and femoral branches have been mapped in detail by Nijenhuis and Dresden (1952, 1955a). In the prothorax 5r1a sends many motor rami to the first (85E), second (85F), third (85G), and fourth (85H) coxal branches of the main depressor of the leg (figs. 2A, B). A very thin branch was followed to the anteromesal coxal wall proximal to the trochanteral articulation (AMCW, fig. 2A). This branch is very likely homologous to its counterpart in the meso- and metathorax (see fig. 3D). Nerve 5r2 was traced to the posterior (dorsal) wall of the meron. Apparently it provides the sensory supply to the setae of this region.

Nerve 5r1b supplies the posterior depressor of the leg (86) as well as the anterior depressor of the leg (87). Only a few of the numerous branches supplying these muscles have been shown in figure 2. Muscle 86 originates on the posterior (dorsal) wall of the coxa and inserts on an apodemal tendon of the trochanter. Muscle 87 originates on the inner part of the anterior (ventral) wall of the coxa and also gives rise to an apodemal tendon of the trochanter.

Nerve 6A: After bending around the episternal muscle of the coxa (97, figs. 2A, B), this nerve courses anteriorly to supply the main tergal remotor of the coxa (81), the tergal remotor of the coxa (80), and the first (76), second (77), third (78), and fourth (79) tergomeral muscles. Muscles 80 and 81 arise from the tergum and go to the basicosta of the coxa. As their names imply, the tergomeral muscles arise from the tergum and insert on the meron. They probably act as remotors of the coxa, too, according to Carbonell.

Nerve 6B: A branch which is homologous to 6Br1 of the meso- and metathorax (see fig. 3C) innervates the spinal muscle of the coxa (98, fig. 2A). Muscle 98 arises from the first spina and passes to a ridge of the prothoracic coxa that begins at the coxopleural articulation. This muscle is homologous to the spinal muscle of the coxa in the mesothorax (134). On the basis of innervation, muscle 134 (see Nijenhuis and Dresden 1955a) would be considered homologous to the second sternal muscle of the coxa (171, fig. 3D). Such homology might not be readily suspected on the basis of myology alone, since 171 passes from a broad origin on the posterior edge of the sternal arm to the ridge which limits the meron, while 134 passes from the second spina to a comparable ridge in the mesothorax.

Nerve 6Br2a innervates the episternal muscle of the coxa (97) which arises from the internal edge of the mesepisternum and passes to the same ridge as muscle 98. Muscle 97 is most likely homologous to the sternal muscle of the coxa (133) in the mesothorax, and the first sternal muscle of the coxa (170, fig. 3D) in the metathorax. Muscles 133 and 170, however, both arise from the end of the sternal arm. They agree with 97 inasmuch as they pass to the ridge which limits the meron near the coxopleural articulation of each segment.

A ramus from 6B which is most likely homologous to 6Br2b of the meso- and metathorax innervates the sternal adductor of the coxa (82, figs. 2A, B). This muscle arises on the sternal arm and inserts on the basicosta of the coxa. On the basis of innervation muscle 82 would be considered homologous to the pleurosternal muscle of the mesothorax (117) (see Nijenhuis and Dresden 1955a) and metathorax (160, fig. 3D). Muscles 117 and 160 differ from 82 in having one of the points of attachment at the pleural arm rather than at the basicosta.

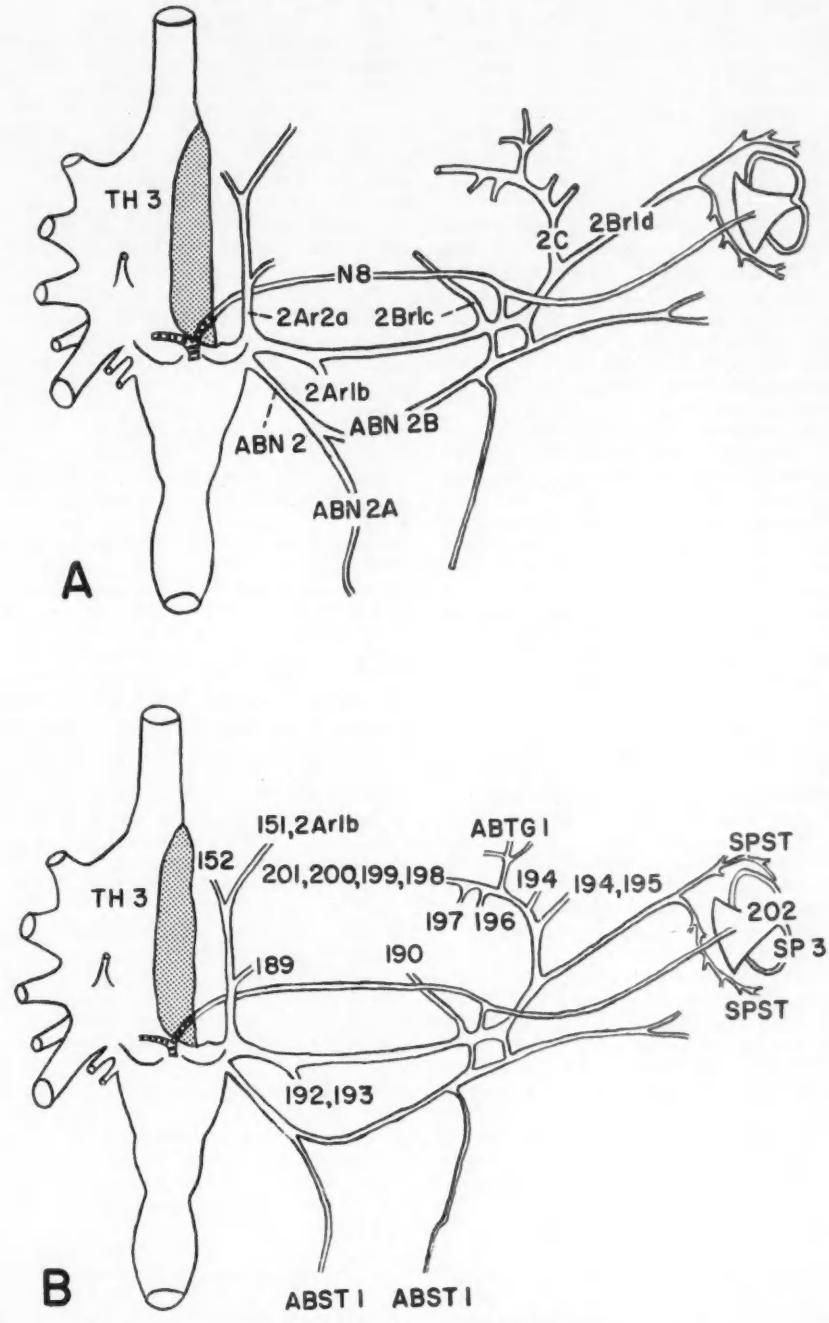
Nerve 6Br3 supplies setae located at the antero-lateral and postero-lateral meron (MER 1, fig. 2A). Though illustrated in ventral view, this nerve is most readily demonstrated by means of a dorsal dissection.

Nerve 6Br4 provides the motor supply of the anterior and posterior branches of the main levator of the leg (88A, 88B). At its most distal extremity in the coxa it supplies the secondary levator of the leg (89), which is a small, presumably weak muscle arising from the posterior (dorsal) coxal wall and inserting on an apodemal tendon of the trochanter. The fusion of 6Br4L with 5r3 which is evident in the meso- and metathorax was not seen in the prothorax. This may be due to its inconspicuousness rather than its absence. For this reason an interrogation mark is placed after "5r3" at the terminus of 6Br4 in figure 2A.

A very thin nerve arises from 6Br4 and apparently is sensory to the antero-distal coxal wall; at least it was followed to the flattened antero-lateral extension of the distal coxa (ADCW, fig. 2A). A homologous nerve was found in the metathorax (ADCW, fig. 3D).

Nerve 7: This is a rather short nerve which has a midlateral origin on the ventral surface of the ganglion (fig. 2A). Apparently it has been overlooked in the past. This is not at all surprising, since it is usually surrounded by fat body and may be removed inadvertently during the preparation of the ventral dissection. Branches from nerve 7 pass anteriorly where they supply the setae of the prothoracic basisternum (BS 1). Posterior branches also innervate the prothoracic furcasternal region (FSR 1). Counterparts of nerve 7 are also found in the meso- and metathorax (fig. 3D).

Nerve 8: This nerve supplies the closing muscle of the first spiracle (107, fig. 1B). The two rami of nerve 8 may share a common origin



EXPLANATION OF FIGURE 4

A. Ventral aspect of sectioned metathoracic ganglion showing nerves of the fused first abdominal ganglion. Peripheral rami are designated.

B. Same as A, but with innervation fields designated.

on the middle posterodorsal surface of the ganglion as shown, or each may arise separately. The first spiracle is usually thought of as belonging to the mesothoracic metamere. The fusion of nerve 8 with certain branches from nerve 2 of the mesothorax will be treated in the section dealing with the mesothoracic ganglion.

NERVES OF THE MESOTHORACIC GANGLION

With the exception of nerves 2, 7, and 8, the distribution of the motor and sensory nerves which issue from this ganglion have been treated in detail by Nijenhuis and Dresden (1952, 1955a).

Nerve 2A: This intercalary nerve branches to form 2Ar1 and 2Ar2 (fig. 1A). The former divides again to form 2Ar1a and 2Ar1b. Nerve 2Ar1a supplies the ventral oblique muscle (102) and the sterno-spinal muscle (99) (fig. 1B). Both of these muscles arise from the prothoracic sternal arm. Muscle 102 extends to the edge of the mesepisternum of the opposite side; 99 to the first spina. Nerve 2Ar1b bifurcates, sending a branch anteriorly and one posteriorly. Each bifurcation rebranches to innervate the ventral longitudinal muscle (100) and the sternal-spinal intersegmental muscle (101). These muscles also arise from the sternal arm of the prothorax. Muscle 100 extends to the mesothoracic sternal arm, 101 to the second spina. Nerve 2Ar2 fuses anteriorly with the interganglionic connective (fig. 1A).

Nerve 2B: Although the three rami which emanate from the proximal part of nerve 2 have separate origins in the mesothorax, homologs to these nerves usually have a common origin in the metathorax (compare 2B, fig. 1A, with that in fig. 3A). It is for this reason that the three rami in the mesothorax are considered as branches of 2B, and not as separate nerves. This is another example of how homologous nerves may not have the same origin in different segments of the same individual.

Nerve 2Br1a supplies the transverse ventral muscle (103, figs. 1A, B) which passes from the first spina to the medial edge of the mesepisternum. The very thin branch 2Br1b fuses with nerve 8. The fact that 2Br1b is a nerve and not a tracheal branch was ascertained by examining it under the phase-contrast microscope. This nerve is composed of one or, at most, a very few axons. Whether 2Br1b passes down nerve 8 and to the prothoracic ganglion, or peripherally to the spiracular region, was not determined.

Nerve 2Br1c gives rise to a very fine branch which innervates muscle Z (MZ, fig. 1B). By gross examination one would hardly suspect that this very thin structure which extends from the midlateral tergum to the ventrolateral membranous area between the prothoracic and mesothoracic segments is a muscle at all. Examination of this structure under the phase-contrast microscope, however, reveals definite cross-striations. It would seem that muscle Z is either a purely rudimentary structure, or an example of a muscle which may be associated with a stretch receptor (Finlayson and Lowenstein 1958). The nature of the small branch from nerve 8 to muscle Z remains unknown. It may, indeed, be a tracheal branch and not a nerve. Homologs to muscle Z were not recognized in the prothorax or metathorax. Anteriorly, the remainder of 2Br1c innervates the phragmal muscle of the sternal arm (96) which extends from the lateral portion of the first phragma to the sternal arm.

Nerve 2Br1d may arise from the remainder of 2Br1 (fig. 1A), or may be fused with it to a varying extent in different individuals. It may be fused with nerve 8 for a considerable distance near its terminus, or be rather widely separated as shown. A branch from 2Br1d passes anteriorly where it also fuses with nerve 8. This branch is most readily seen when the rest of 2Br1d is separated from nerve 8. It is very likely that it continues anteriorly after fusing with nerve 8 and is seen once again as the nerve which provides the sensory supply for the postero-pleural ridge (PPR, fig. 1B). The remainder of nerve 2Br1d supplies the setae (SPST) which are located dorsal and ventral to the first spiracular opening.

Nerve 2Br2 bifurcates at its distal end to form 2Br2a and 2Br2b. Nerve 2Br2a supplies the numerous setae of the first tegula (TGA 1, fig. 1B) which is located at the anterior edge of the base of the fore wing. On the basis of its very generous nerve supply and its location, it would appear that the tegula serves an important proprioceptive function. Nerve 2Br2b divides to form branches which were traced into the basal parts of the larger anterior veins of the fore wing and branches which are apparently sensory to the immediate region of the axillary sclerites (W, AXR).

Nerve 2C: This nerve provides the motor supply of the dorsal longitudinal muscle (110), the first oblique dorsal muscle (111), the second oblique dorsal muscle (112), and the third oblique dorsal muscle (113). It is also sensory to the mesothoracic tergum (TRG 2, fig. 1B).

Nerve 7: This nerve is not represented among the accompanying illustrations. It occupies the same relative position on the mesothoracic ganglion as do its homologs in the pro- and metathorax (figs. 2A, B; 3D). In the mesothorax, as in the other two segments, it supplies the setae of the basisternum as well as the furcasternal region.

Nerve 8: As in the prothorax, this nerve supplies the spiracular closing muscle in the succeeding segment (147, fig. 3B). Its fusion with certain branches from nerve 2 of the metathorax will be treated in the following section.

NERVES OF THE METATHORACIC GANGLION

Nerve 2A: This nerve branches to form 2Ar1

and 2Ar2 (fig. 3A). A very thin nerve leaves 2Ar1 and passes posteriorly to supply the spinosternal muscle (189) and the spinosternal oblique muscle (151). This nerve could not be homologized with a mesothoracic counterpart. As their names imply, 151 and 189 arise from the second spina. Muscle 189 passes to the second abdominal sternum; 151 to the anterior edge of the sternal arm. Another very thin branch passes from nerve 2Ar2a to nerve 2Ar1. This is most readily revealed by means of a ventral dissection.

Nerve 2Ar1b (fig. 3A) branches anteriorly and posteriorly to supply the ventral longitudinal muscle (148, fig. 3B). This muscle extends from the sternal arm of the mesothorax to that of the metathorax. Another branch from 2Ar1b was traced anteriorly to where muscles 100, 104, and 125 join the basal part of the sternal arm (JSA, fig. 3B). It is not clear whether any of these muscles are innervated by this branch. Posteriorly, this same branch also fuses with a segment of 2Ar2a (see 151, 2Ar1b, fig. 4B). Externally, at least, the product of this fusion appears to supply muscles 151, 189, and the spinosternal longitudinal muscle (152). The innervation of muscles 151, 189 and 152 will be treated in more detail under the discussion of the distribution of the rami of the first abdominal ganglion. Nerve 2Ar2 fuses with the interganglionic connective.

Nerve 2Ar2a arises at the junction of 2Ar2 and the interganglionic connective. It gives rise to branches which innervate the sternal-spinal intersegmental muscle (101), the spinosternal muscle (104), and the spinal longitudinal ventral muscle (106). As mentioned previously 101 is also innervated by a branch of 2Ar1b in the mesothorax. Muscle 104 passes from the first spina to the base of the mesothoracic sternal arm; 106 from the first to the second spina.

Nerve 2B: A bifurcation of this nerve gives rise to 2Br1 and 2Br2. The former branches again to form 2Br1a which innervates the transverse ventral muscle (149, fig. 3B). This muscle courses from the second spina to a small plate near the edge of the metepisternum. Nerve 2Br1b fuses with a ramus from nerve 8 of the mesothorax. This very thin nerve appears to pass down nerve 8 to the mesothoracic ganglion. The fact that 2Br1b is a nerve and not a tracheal branch was ascertained with the phase-contrast microscope. Nerve 2Br1c supplies the phragmal muscle of the sternal arm (125), which originates on the lateral aspect of the second phragma and terminates on the upper surface of the basal part of the sternal arm.

Nerve 2Br1d fuses distally with a branch of nerve 8 (fig. 3A). It probably continues anteriorly to provide the sensory supply of the posteropleural ridge (PPR, fig. 3B). The sparse spiracular setae located ventral to the metathoracic spiracle (SPST) are probably also supplied by a branch of 2Br1d. This branch is much less conspicuous here than it is in the mesothorax, however.

Nerve 2Br2a supplies the tegula of the metathoracic wing (TGA 2). A branch from this nerve also supplies the numerous setae of the dorsal and anterolateral spiracular sclerite (SPST). In the mesothorax this branch is absent, the corresponding regions being supplied by branches from 2Br1d. As in the mesothorax, 2Br2b innervates the wing itself and apparently the region of the axillary sclerites as well (W, AXR, fig. 3B).

Nerve 2C: This nerve branches to supply the dorsal longitudinal muscle (153), and the first (154), second (155), and third (156) dorsal oblique muscles. Muscle 153 passes from the second phragma to the first abdominal tergum. Muscles 154 through 156 pass from various points on the metatergum to the first abdominal tergum. This nerve also sends sensory branches to the metatergum (TRG 3).

Nerve 3A: The first anterior branch, 3Ar1, consists of 3Ar1a and 3Ar1b which may be separated at their bases (fig. 3A), or fused as indicated by Nijenhuis and Dresden (1955a). Nerve 3Ar1a supplies the setae of the first plate of the metathoracic episternum (3EPS 1, fig. 3B). Nerve 3Ar1b fuses with a branch of 6Ar4 (figs. 3C, D). Superficially, at least, the product of this fusion appears to innervate muscles 157, 158, and 159. The points of attachment of these muscles will be treated under the discussion of nerve 6A.

A metathoracic counterpart of 3Ar2a of the mesothorax (Nijenhuis and Dresden 1955a) was not found. This is not surprising, since the homolog of the phragmal muscle of the basisternum (121) which is supplied by this nerve in the mesothorax is absent in the metathorax. Nerve 3Ar2b (fig. 3A) sends branches to the first and second episternal muscles of the trochantin (164, 165, fig. 3B). These muscles arise near the anterior edge of the episternum and insert on the first plate of the trochantin. The innervation of the very thin third episternal muscle of the trochantin (166) was not established.

Nerve 3Ar2c supplies the first and second episternal promotors of the coxa (167, 168). Muscle 167 originates on the anterior margin of the episternum and inserts ventrally on the anterior edge of the ventral wall of the coxa, between the epimeral and trochantinal articulations. Muscle 168 originates on the posterolateral episternum and the under surface of the pleural ridge and pleural arm, inserting on an apodemal tendon attached to a small plate near the edge of the coxa and the coxopleural articulation.

Nerve 3Ar3 (fig. 3A) sends numerous branches to the first (161), second (162), and third (163) tergal muscles of the trochantin. As their names

imply, these muscles arise from the tergum and insert on the first plate of the trochantin. A branch of 3Ar3 also innervates the phragmal muscle of the episternum (150) and muscle PEP (fig. 3B). The latter has not been indicated by Carbonell. It passes from the second phragma to the anterior metathoracic episternum, as does muscle 150. In all likelihood, muscle PEP corresponds to one of the phragmal muscles of the mesothoracic episternum (108 or 109).

Nerve 3B: The description of the distribution pattern of this nerve in the prothorax will also serve here with very little modification. The major difference lies in the fact that certain of the coxal rami of this nerve (3Br6, 3Br7, fig. 3A) supply the anterior coxal levator of the leg (180, fig. 3B). Muscle 180 originates on the anterior coxal wall and inserts on an apodemal tendon attached to the anterior part of the distal half of the trochanter.

Nerve 4: As in the other metameres, it would seem that this nerve serves a purely motor function. Nerve 4r1a supplies the spinal muscle of the coxa (173); 4r1b, muscle MX 3 (figs. 3C, D). Muscle 173 originates on the second spina and inserts on the anterior wall of the coxa. On the basis of innervation, this muscle would be considered homologous to the spinal rotator of the middle coxa (105, Nijenhuis and Dresden 1955a). MX 3 arises from a very small sclerite in the membranous cuticle of the anterolateral furcasternal region and passes to the coxal rim where the second trochantin articulates.

Nerve 4r2 supplies the sternal remotor of the coxa (172) and the sternal branch of the main depressor of the leg (177B). Muscle 172 originates on the posterior edge of the sternal arm and inserts on the posterior (dorsal) coxal rim. Muscle 177B passes from the anterior margin of the sternal arm to a broad apodemal tendon attached to the proximal angle of the trochanter.

Nerve 4r3 sends numerous rami to the tergal branch of the main depressor of the leg (177A) and the basalar muscle of the forewing (177C). Muscle 177A arises from the anterior tergum, 177C from an apodemal tendon arising from the edge of the basalar plate which articulates with the episternum. Both of these muscles pass to the same apodemal tendon as muscle 177B.

Nerve 5: Nerve 5r1a ramifies to the first (177D) and second (177E) coxal branches of the main depressor of the leg. Muscle 177D originates on the mesal angle of the coxa, 177E on the anterior wall of the coxa and anterior coxal rim. Both of these muscles pass to the same apodemal tendon as 177A, B, and C. In addition to these motor branches, this nerve sends sensory fibers to the anteromesal coxal wall (AMCW, fig. 3D).

Nerve 5r1b redivides many times to supply the posterior (178) and anterior (179) coxal depressors of the leg. All of the branches are not indicated in figures 3C or 3D. Muscle 178 originates on the posterior wall of the coxa and the posterior coxal rim, and inserts on an apodemal tendon attached to the posterior part of the proximal end of the trochanter. Muscle 179 arises on the anterior coxal wall and anterior coxal rim, and inserts on an apodemal tendon attached to the anterior part of the proximal end of the trochanter.

Nerve 5r2 (fig. 3C) provides the sensory supply of the posterior (dorsal) wall of the meron (PM 3, fig. 3D). Branch 5r3 fuses with a ramus from nerve 6B at the distal end of the coxa (see 182A, 5r3, or 182A, 6Br4L, fig. 3D). Certain components of this fusion probably innervate a branch of the posterior coxal levator of the leg (182A).

Nerve 6A: The first branch of this nerve, 6Ar1 (fig. 3C) sends numerous rami to the second and third tergal remotors of the coxa (175, 176, fig. 3D). These muscles originate on the anterior metatergum and insert on the posterior part of the coxal rim. The first tergal remotor of the coxa (174) has a similar origin and insertion, but is innervated by 6Ar3. Nerve 6Ar2 branches to the subalar muscle of the hind wing (169). This powerful muscle originates on the meron and inserts on the subalar plate.

A branch of 6Ar4 fuses with 3Ar1b as was mentioned in the treatment of the distribution of nerve 3A. Superficially, at least, the product of this fusion appears as if it might innervate any or all of the following: the tergopleural muscle (157), the pleuroalar flexor of the wing (158), and the tergopleural muscle (159). Muscle 157 passes from the lateral tergum to the upper surface of the pleural ridge; 158 from the pleural ridge to the third axillary sclerite. Muscle 159 goes from the anterior edge of the pleural arm to a part of the anterior notal wing process which articulates with the first axillary sclerite. Nerve 6Ar4 was once seen arising adjacent to 6Ar1. This origin is indicated by a broken pattern in figures 3C and 3D.

Nerve 6B: Branches 6Br1 and 6Br2 may arise separately as described in the mesothorax by Nijenhuis and Dresden (1955a) or they may be fused and arise from 6B as a single ramus (i.e., as in fig. 3C). Nerve 6Br1 supplies the second sternal muscle of the coxa (171) which originates on the posterior edge of the sternal arm and inserts on the ridge which limits the meron. The first sternal muscle of the coxa (170) is innervated by 6Br2a (figs. 3C, D). Muscle 170 originates on the end of the sternal arm and also inserts on the ridge which limits the meron. Nerve 6Br2b supplies the pleurosternal muscle (160), which goes from the anterior edge of the pleural arm to the anterior edge of the sternal arm. This nerve may also arise as a separate branch from 6B, as indicated by the broken pattern in figures 3C and 3D.

Nerve 6Br3 provides the sensory innervation of the anterolateral and posterolateral walls of the meron (MER 3, fig. 3D). It is most readily demonstrated by means of a dorsal dissection. Branch 6Br4 redivides many times to innervate the posterior branch (181A), and the first (181B) and second (181C) anterior branches of the main levator of the leg. As their names imply, these branches originate either on the posterior (dorsal) or anterior (ventral) walls of the coxa and converge on an apodemal tendon attached to the distal trochanter. A very fine nerve, apparently sensory in function, emanates from 6Br4. It was traced to the flattened anterolateral extension of the distal coxa (ADCW, fig. 3D). Various branches of the posterior coxal levator of the leg (182B, C, D) are also innervated by fibers from 6Br4. Muscle 182A is innervated by a branch resulting from the fusion of 6Br4L with 5r3 (see 182A, 5r3, fig. 3D). The various branches of muscle 182 have different origins on the posterior (dorsal) coxal wall and insert on an apodemal tendon which is attached to the trochanter near the insertion of muscle 181.

Nerve 7: As in the pro- and mesothorax, this nerve supplies the basisternum (BS 3) and furcasternal region (FSR 3) (fig. 3D).

Nerve 8: The closing muscle of the first abdominal spiracle (202, fig. 4B) is supplied by this nerve.

NERVES OF THE FIRST ABDOMINAL GANGLION

The metathoracic ganglion is fused with the first abdominal ganglion. This fusion accounts for the presence of the two additional nerves emanating from this region.

Nerve 2Ar2a: The first of these abdominal nerves sends a branch anteriorly which subdivides to innervate the spinosternal muscle (189, fig. 4B), the spinosternal oblique muscle (151), and the spinosternal longitudinal muscle (152). As their names imply, these muscles arise on the second spina. Muscle 189 passes to the second abdominal sternum, 151 and 152 to different parts of the metathoracic sternal arm. As mentioned previously, a segment of this abdominal nerve fuses with a branch of 2Ar1b from the metathorax (see 151, 2Ar1b, fig. 4B). Muscle 189 appears to be homologous to muscle 106, 151 to 101, and 152 to 104. Muscles 106, 101, and 104 are innervated by nerve 2Ar2a of the metathorax. For this reason this branch of the first abdominal nerve is also designated as 2Ar2a.

Nerve 2Ar1b: This branch of the first abdominal nerve supplies the first and second longitudinal ventral muscles (192, 193). These muscles arise on the under surface of the sternal arm. Muscle 192 passes to the anterior edge of the first abdominal sternum; 193 to that of the second. It is probable that these muscles are, at least in part, homologous to the ventral longitudinal muscle of the metathorax (148, fig. 3B). It is for this reason that the nerve supplying muscles 192 and 193 is designated as 2Ar1b (figs. 4A, B).

Nerve 2Br1c: The tergosternal muscle (190) which passes from the upper surface of the sternal arm to the first abdominal tergum is innervated by this ramus. This muscle appears to be homologous to the phragmal muscle of the sternal arm (125) which also arises from the upper surface of the sternal arm, but passes to the lateral part of the second phragma.

Nerve 2Br1d: As in the mesothorax, this nerve clearly supplies setae located dorsal and ventral to the first abdominal spiracle (SPST, fig. 4B).

Nerve 2C: Muscles 194 through 201 are abdominal muscles which have not been considered by Carbonell. The two most proximal branches of 2C innervate muscles 194 and 195 (figs. 4A, B). Both of these muscles arise from the lateral antecosta of the first abdominal tergum. Muscle 194 courses posteromedially and attaches to the antecosta of the second abdominal tergum, 195 posterolaterally. Muscle 195 appears to be composed of two branches. Whether these should be considered as separate muscles or not is questionable.

Muscle 196 is very short, extending from the posterior middle and midlateral tergum of the first abdominal segment to the lateral antecosta of the second abdominal segment. Muscle 197 is thin and also passes from the midlateral tergum of the first abdominal segment to the antecosta of the second abdominal segment. Muscles 198 through 201 pass from the antecosta of the first abdominal tergum to that of the second. Of the muscles 197 through 201, 197 is the most lateral, 201 the most medial. Nerve 2C is so designated because it is believed that at least some of these abdominal muscles are homologous to the longitudinal and oblique dorsal muscles of the three thoracic metameres. A branch from 2C also redivides to send numerous rami to the tergum of the first abdominal segment (ABTG 1, fig. 4B).

Nerve ABN 2: This second nerve of the first abdominal ganglion could not be homologized with any nerve investigated in the thorax. ABN 2A (fig. 4A) can be traced to a very thin muscle which extends between the anterior edges of the first and second sternites of the abdomen. Very thin branches of this nerve were also traced to the cuticle of the first abdominal sternum (ABST 1, fig. 4B).

The branches of ABN 2B are numerous and very thin. The association of most of these branches with fat body and tracheae obscures the nature of their ramifications. One branch can be traced to the cuticle of the first abdominal sternum (ABST 1, fig. 4B). Fusion of a ramus of ABN 2B with a branch of the first nerve of the first abdominal ganglion is evident.

DISCUSSION

The suboesophageal ganglion gives rise to a nerve which supplies two muscles (52, 53). These probably act as retractors of the head (Carbonell 1947). Such innervation by fibers originating in the head has been described in numerous other insects (Holste 1910; Marquardt 1939; Wittig 1955; Matsuda 1956; Nüesch 1957; Henry 1958). The suboesophageal nerve may or may not be fused with the intercalary nerve or a prothoracic nerve. This depends, apparently, upon the particular species concerned.

A prothoracic nerve, here termed the chiasmic nerve, has been pictured by Matsuda (1956), who states that it innervates a muscle which passes from the ventral cervical sclerite to the postmandibular ridge. In *Periplaneta* it would appear that this nerve serves a proprioceptive function especially related to head and coxal movement.

Nerve 2A in the prothorax supplies muscle 55 which probably functions as a retractor of the head. In the meso- and metathorax various branches of this nerve supply muscle 99 and so-called intersegmental muscles (100, 101, 102, 104, 106). When one considers the points of attachment of these intersegmental muscles and also such muscles as 148, 151, 152, and 189, it is tempting to postulate that they are involved primarily with the maintenance of posture, rather than locomotion. It would be interesting to examine the nature of the stimuli transmitted to these muscles to determine whether they are entirely of the "slow" variety as proposed for postural maintenance by Pringle (1939).

Nerve 2B in the meso- and metathorax is primarily sensory to the spiracular region, tegula, wing, axillary region, and posterior pleural region. The spiracular setae are apparently functional as mechanoreceptors, for by stimulating them Case (1957) could incite closure of the spiracles.

Nerve 2C in all three thoracic segments supplies the dorsal longitudinal and dorsal oblique muscles. This nerve appears to be a rather constant feature of the insect thorax (Holste 1910; Maki 1936; Marquardt 1939; Wittig 1955; Matsuda 1956; Nüesch 1957). It is also sensory to the respective terga in *Periplaneta*.

The prothoracic nerve 3Aprl has no obvious homolog in the meso- or metathorax. It provides the sensory supply of the first and second cervical plate. It also supplies muscles 57 and 58 which, according to Carbonell (1947), possibly act by pulling the upper head back, thereby bringing the mouthparts foreward.

In the prothorax nerve 3A provides sensory branches to the tergum, epimeron, episternum (in certain individuals), and a small setiferous sclerite located just anterior to the pleural ridge and slightly ventral to the anterolateral protergum. In the meso- and metathorax the sensory role of 3A appears limited to an innervation of the first plate of the episternum. In all three segments nerve 3A is comprised of fibers which supply coxal adductors and promotors. In the meso- and metathorax a branch from 3A fuses with a branch from 6A. This fusion supplies the tergopleural muscles, and the pleuroalar flexor of the wing.

Nerve 3B comprises the major sensory supply of the coxa. It innervates hair plates and chordotonal organs, as well as the coxal setae. In the meso- and metathorax it also supplies the anterior coxal levator of the leg (138, 180). Distally it fuses with nerve 5 in all three metameres.

Nerve 4 supplies the main depressor of the leg in all three metameres. A branch of this main depressor (135C, 177C) probably serves as a promotor and extensor of the wings (Carbonell 1947). Nerve 4 also supplies certain coxal remotors (83, 132, 172), and muscles which probably act as adductors and rotators (105, 173). The gross anatomy of the distribution of nerve 4 would lead one to conclude that it is strictly a motor nerve.

In the coxa, nerve 5 is sensory to the posterior meron. It also supplies the setae of the anteromesal coxal wall. The coxal branches of the main depressor of the leg are supplied by rami from nerve 5. In this fashion it is synergistic to nerve 4. It innervates the coxal depressors of the leg as well. Distally, a branch of nerve 5 fuses with a branch from 6B.

Nerve 6A sends branches to numerous remotor muscles of the coxa. In the meso- and metathorax it also innervates the depressor-extensor muscle of the wing (128, 169). In other insects, at least, this muscle is recognized as important in powering the downstroke of the wing (Carbonell 1947). The fusion of a part of 6A in the meso- and metathorax with a branch from 3A was discussed previously.

The major levator muscles of the legs are innervated by branches from 6B, as are muscles which probably function as coxal rotators or rotator-adductors (97, 98, 133, 134, 170, 171). A very fine branch from 6B also supplies the setae of the anterodistal coxal wall.

Nerve 7 appears to be purely sensory in function, supplying the setae of the basisternum and furcasternal region in each metamere. The *nervus sternalis* described by Holste (1910) in *Dytiscus marginalis* appears to be homologous to this nerve.

The eighth or median nerve appears to be another very constant feature of the hexapod nervous system (Holste 1910; Maki 1936; Marquardt 1939; Wittig 1955; Nüesch 1957). Its role as a regulator of the spiracular opening in *Periplaneta americana* and *Blaberus craniifer* has been established by Case (1957).

The first abdominal ganglion and metathoracic ganglion are fused. Two distinct nerves emanate from the abdominal component. Various rami

of the first have been homologized with the second nerve of the thoracic ganglia. The distribution of the second of these abdominal nerves is largely obscured because of its thinness and very close association with fat body.

The existence of a fundamental plan in the peripheral distribution of the thoracic nerves of even widely separated insect orders cannot be denied. Indeed, Wittig (1955) has constructed a table which compares the innervation fields of the thoracic nerves of *Perla abdominalis* (Plecoptera) with those of *Chauliodes formosanus* (Neuroptera), as reported by Maki (1936), *Carausius morosus* (Phasmodea) as reported by Marquardt (1939), and *Dytiscus marginalis* (Coleoptera) as reported by Holste (1910). Despite unfortunate differences in the nomenclature applied by different workers, the existence of nerve homologies in these widely separated insects has been made obvious. It is not surprising that, basically, the pattern of distribution in *Periplaneta americana* agrees with that found in other insects which have been investigated. This has been indicated by Nijenhuis and Dresden (1955b) as well.

Notwithstanding the presence of a fundamental pattern of distribution, it is not always an easy matter to establish nerve homologies without undertaking a thorough examination of the many branches of each nerve. This is true because considerable modification has been superimposed on the fundamental pattern.

Nerve fusions can and most certainly do occur. Such fusions contribute greatly to the apparent variations noted in the nerve distribution patterns of different insect groups. Indeed, a rather marked degree of variability in such fusion can be found between individuals of the same species as well as between different segments of the same individual.

Though this study is not intended primarily as a contribution to comparative morphology, a note of caution might well be introduced here. The highly optimistic feeling that a knowledge of the gross anatomy of nerve distribution will, by itself serve as a panacea to the difficulties encountered in attempts to homologize muscles appears untenable. There is no sound basis for the presumption that nervous systems have remained any more static in their phylogenetic development than muscles or exoskeletons. Indeed, the available information indicates that a remarkable degree of modification has occurred.

These difficulties are compounded by the finding that muscles which appear to be an integrative part of one segment may be innervated by nerve fibers which arise from the ganglion of another segment as well. This has been experimentally demonstrated by Nüesch (1954) in *Telea polyphemus*. By cutting certain nerves in diapausing pupae, he noted that the muscles normally supplied by these nerves failed to generate in the adult. In this way he was able to show that certain components of the dorsal longitudinal flight muscles of the mesothorax are innervated by fibers which originate in the prothoracic ganglion as well as by fibers originating in the mesothoracic ganglion. The prothoracic fibers apparently pass to the longitudinal flight muscles via the intercalary nerve.

An histological examination of the intercalary nerve of *Periplaneta* reveals that it is largely comprised of very coarse fibers which pass from the preceding ganglion of each thoracic segment to nerve 2C, and thence peripherally. It is highly probable that these are the axons of neurocytes located in the preceding segment and destined to innervate certain of the dorsal longitudinal muscles of the following segment. It appears that these fibers may be comparable to those demonstrated experimentally by Nüesch.

Marquardt (1939) pictures a nerve which originates in the prothoracic ganglion of *Carausius morosus* and which seems to be homologous to the intercalary nerve of other insects. Perhaps this nerve also contains fibers comparable to those demonstrated by Nüesch.

The present investigation indicates that the sternal-spinal-intersegmental muscle (101), the spinosternal muscle (189), and the spinosternal oblique (151) and longitudinal (152) muscles may be innervated by fibers originating in more than one ganglion.

The presence of fusions between nerves which originate in different ganglia also complicates the problem of establishing muscle homologies on the basis of innervation. More comparative studies may clarify this problem to some extent, but recourse to a histological approach may also become necessary.

REFERENCES CITED

Carbonell, C. S. 1947. The thoracic muscles of the cockroach *Periplaneta americana* (L.). Smithsonian Misc. Coll. 107(2): 1–23.

Case, J. F. 1957. The median nerve and cockroach spiracular function. Jour. Ins. Physiol. 1: 85–94.

Finlayson, L. H., and **O. Lowenstein.** 1958. The structure and function of abdominal stretch receptors in insects. Proc. Roy. Soc. London (B) 148: 433–49.

Henry, L. M. 1958. Musculature of the cervical region in insects. Microentomology 23: 95–105.

Holste, G. 1910. Das Nervensystem von *Dytiscus marginalis*. Zeitschr. wiss. Zool. 96: 419–76.

Maki, T. 1936. Studies of the skeletal structure, musculature, and nervous system of the alder fly *Chauliodes formosanus* Petersen. Mem. Fac. Sci. Agric. Taihoku Imp. Univ. 16: 117–243.

Marquardt, F. 1939. Beiträge zur Anatomie der Muskulatur und peripheren Nerven von *Carausius* (*Dixippus*) *morosus* Br. Zool. Jahrb. (Anat.) 66: 63–128.

Matsuda, R. 1956. The comparative morphology of the thorax of two species of insects. Microentomology 21: 1–65.

Nijenhuis, E. D., and **D. Dresden.** 1952. A micromorphological study of the sensory supply of the mesothoracic leg of the American cockroach, *Periplaneta americana*. Proc. K. Nederland. Akad. Wetenschap. (C) 55: 300–10.

1955a. On the topographical anatomy of the nervous system of the mesothoracic leg of the American cockroach (*Periplaneta americana*). I. Ibid. 58: 121–30.

1955b. On the topographical anatomy of the nervous system of the mesothoracic leg of the American cockroach (*Periplaneta americana*). II. Ibid. 58: 131–6.

Nüesch, H. 1954. Segmentierung und Muskelinnervation bei *Telea polyphemus* (Lepid.). Rev. Suisse Zool. 61: 420–8.

1957. Die Morphologie des Thorax von *Telea polyphemus* Cr. (Lepid.). II. Nervensystem. Zool. Jahrb. (Anat.) 75: 615–42.

Power, M. E. 1943. The effect of reduction in numbers of ommatidia upon the brain of *Drosophila melanogaster*. Jour. Exptl. Zool. 94: 33–72.

1946. An experimental study of the neurogenetic relationship between optic and antennal sensory areas in the brain of *Drosophila melanogaster*. Jour. Exptl. Zool. 103: 429–62.

Pringle, J. W. S. 1939. The motor mechanism of the insect leg. Jour. Exptl. Biol. 16: 220–31.

Wittig, G. 1955. Untersuchungen am Thorax von *Perla abdominalis* Burm. (Larve und Imago). Zool. Jahrb. (Anat.) 74: 491–570.

POPULATION FLUCTUATIONS OF THE EUROPEAN CORN BORER, PYRAUSTA NUBILALIS, AT WASECA, MINNESOTA, 1948 TO 1957[1]

H. C. CHIANG[2] AND A. C. HODSON[3]

ABSTRACT

The abundance of the various stages in the borer population fluctuated in a random manner. Young larvae always suffered high mortality and few of them reached maturity, even under the most favorable conditions. Of the biological events recorded, percent of summer pupation showed the greatest variability, hence might be a more important determinant of the direction and magnitude of borer-population fluctuations than the larval mortality. The quantitative relationships of the summer and fall populations in a given year are affected by the size of the first-generation population, the amount of summer pupation, and the favorability of the environment for development and survival of the second generation. A summer mature larval population of any given size might give rise to a fall population many times larger, or to one only a fraction of the original size. Fluctuations of the populations of different life stages followed different patterns, so that the mean interval between two successive peaks of abundance was not the same for all stages. Fluctuation of all stages within years and between years was so haphazard as to suggest an independence of each other and a dependence upon the equally haphazard vagaries of the weather. The population dynamics of the species in southern Minnesota suggest that here it is occupying a fringe area in its distribution, where the relatively harsh climate produces random fluctuation at a relatively low level of abundance. Competetive mechanisms seem not to have been important in determining either the population levels or their fluctuations.

Since its establishment in this country in 1910, the European corn borer has spread throughout the eastern states and the corn belt of the north central region. Because of its great economic importance, the population fluctuations of this insect and their relation to environmental factors have been studied by many workers in different areas.

Stirrett (1938) concluded, after 10 years' work, that the factors causing population fluctuations are complex, and, in many cases, interdependent. Huber et al. (1928) stated that "Until all factors are properly evaluated either individually, in combination, or perhaps both, it will be quite impossible to state definitely the extent of distribution, accumulation, fluctuation and other responses of the European corn borer are due to any single factor." Some 20 years later, Neiswander (1952) again stated, "There are a great many factors that influence borer accumulation, many of which cannot be, or at least have not been, properly evaluated because of their complexity. In many instances the overall result is produced by the interaction of a number of environmental factors." Thus while the earlier works called attention to the effect of a number of factors, most authors suggested that (1) the factors studied do not represent all the factors which influence the borer populations, (2) the effects of the factors studied do not represent all the effects which these factors may have exerted on the borer populations, (3) the evaluations are only on a general and qualitative basis, and (4) in cases where the effect was evaluated quantitatively, the validity of such evaluation is usually limited strictly to the specific situations studied. In other words, because of the great diversity of the environmental factors and the great complexity of the operation of such factors, few generalizations on the population dynamics of the corn borer may be drawn from studies on the effect of individual environmental factors.

A continuous study has been carried out in southern Minnesota since 1948 to investigate the population changes of the European corn

[1]Paper No. 4082, Scientific Journal Series, Minnesota Agricultural Experiment Station, St. Paul 1, Minnesota. Accepted for publication March 11, 1959.

[2]Associate Professor, University of Minnesota, Duluth 11.

[3]Professor, University of Minnesota, St. Paul 1.

Table 1.—Population levels of various stages of the European corn borer in Waseca, Minn., 1948 through 1957. (All data expressed on the basis of number per 100 plants)

Year	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957
First generation										
Number of egg masses	26	174	380	121	11	28	19	0	22	25
Number of eggs	380	2395	5798	1754	151	448	204	0	376	28
Number of young larvae	326	1495	2973	925	85	287	167	0	281	28
Number of larvae matured	57	150	434	135	41	39	21	0	28	7
Number of larvae pupated	10	138	24	13	10	19	10	0	19	4
Second generation										
Number of egg masses	46	217	18	19	175	26	44	22	47	38
Number of eggs	762	5049	290	311	2980	478	570	350	778	502
Number of young larvae	329	3266	265	164	1565	309	520	238	672	281
Number of larvae matured	64	134	0	0	34	24	2	16	9	21
Fall population										
Number of borers	111	147	410	122	59	39	13	16	18	25

borer and the effect of environmental factors upon them. The present paper deals with population changes as responses to the whole environment, and reports studies made at the Experiment Station, University of Minnesota, Waseca, Minnesota, during the growing seasons of 1948 to 1957, inclusive.

MATERIAL AND METHODS

Host Plants.—Fields of Minhybrids which are commonly grown in the area were planted during the early part of the normal period of planting for the particular seasons. Normal farm procedures of crop rotation, soil management, and cultivation were followed. One field was under observation in each of the 10 years.

Counting the Egg Mass Population.—Various numbers of plants were marked at the beginning of the season. These plants were distributed throughout the field. They were checked about every 3 to 5 days during the egg deposition period of both the first and second generations. Egg masses found at each examination were marked so they could be checked again until the eggs hatched, died, or were dislodged. The number of eggs in each mass and the number of eggs that hatched during each generation also were recorded. The average number of eggs in the field was computed for each field.

Estimating Larval and Pupal Populations.—A number of plants were dissected at intervals to determine the survival and the development of borers throughout the season. Particular emphasis was given to the number of larvae which reached maturity and pupated during the summer, and the number which reached maturity in the fall. The method of differentiating between larvae of the two generations in the fall has been described in an earlier report (Chiang and Hodson 1952).

RESULTS

The populations of the various stages were computed on the basis of the number of individuals per 100 plants. They are shown in table 1, and also in figure 1. Since the variation in numbers covered a wide range (from less than 10 to more than 5,000), the numbers of individuals are arranged in the graph on a logarithmic scale. It is also to be noted in the graph that some of the first generation mature larvae, those which did not pupate in midsummer, persisted through the latter part of the season to become a part of the fall population (black part of last column in each year group).

Examination of table 1 and figure 1 will show that the borer populations changed greatly both within a given year and throughout the 10-year period. These changes will be discussed in three aspects: (1) changes among the different life stages of the same generation in a given year, (2) changes among the two generations of the same year, and (3) fluctuations throughout the 10-year period. Special computations and comparisons of different portions of the basic results as presented in table 1 were made to elucidate these three aspects of the population changes.

POPULATION CHANGES AMONG THE DIFFERENT LIFE STAGES OF THE SAME GENERATION

In Minnesota there are two generations of the European corn borer annually. In the following discussion the changes in abundance of the different stages within each generation are followed through from the egg stage. Because the mortality of the various successive stages is different, the rate of change of the populations during either generation of a given year may vary from stage to stage and from year to year. To facilitate comparisons, data from table 1 are trans-

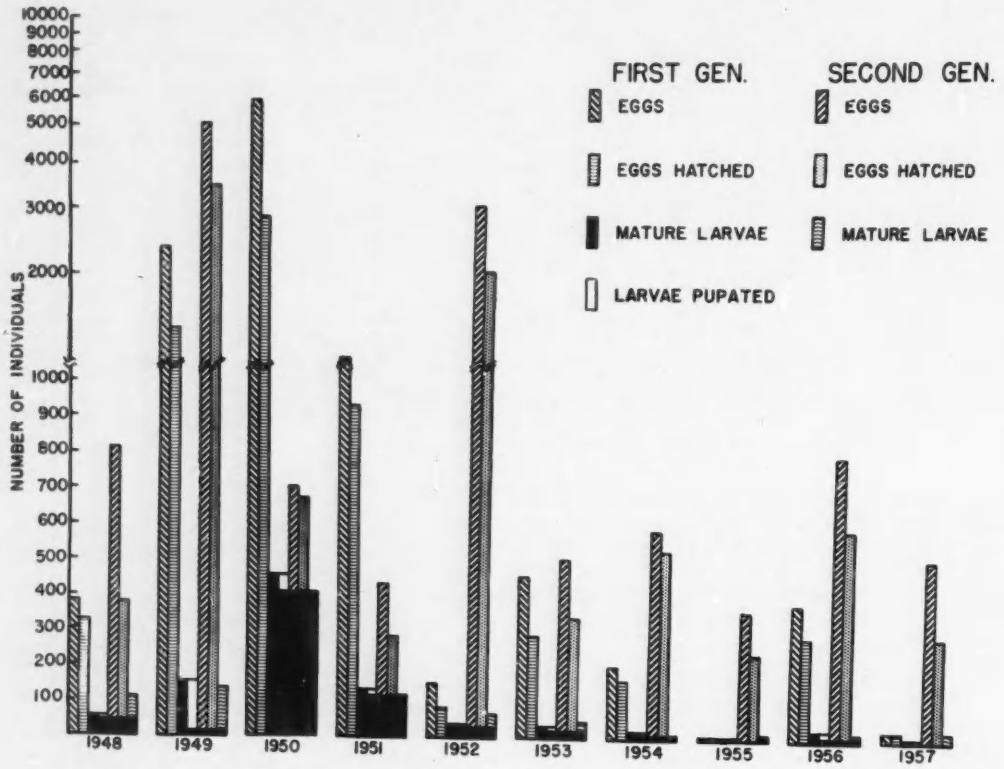


FIG. 1.—Fluctuations of corn-borer populations of various stages at Waseca, Minnesota, 1948 to 1957.

formed in table 2 and are graphed in figures 2 and 3. The populations of the various life stages are plotted against the number of egg masses. Because of the wide range of numbers, the ordinates are plotted on a logarithmic scale. In both generations it can be seen that the number of eggs and the number of young larvae are fairly well correlated with the number of egg masses. This is a confirmation of the findings by Chiang and Hodson (1952) on the basis of more limited data. The numbers of mature larvae and pupae, however, were not as well correlated with the initial number of egg masses. This point is further elucidated by the analyses presented in table 3. For this table, the size of the egg masses, the percent hatch, the percent of successful development of larvae to maturity, and the percent of pupation for both generations were calculated from the data in table 1. The means for the 10-year period are also given. It can be seen that the standard deviation of the means and the coefficient of variation were much greater for larval development and pupation than for the size of egg masses and success of hatching.

This explains the lack of correlation between the number of egg masses and the mature larval population, and between the number of masses and the pupal population. Furthermore, the coefficients of variation of larval development and pupation were so great that the 10-year averages have no predictive value. But the high degree of variability is itself a very important characteristic of borer population dynamics. To facilitate further analyses of this point, the percentages given in table 3 are presented in figure 4. To avoid crowding the graph, data are presented for only 5 of the 10 years. The different events are arranged from left to right in the sequence they occur during the season. For a given event, the years are arranged from top to bottom according to their percent values. The percent values for the different events in a given year are connected by lines. By following the lines one can see the relative ranking of that year among the 5 years illustrated. For example, 1950 ranked extremely low in all events except the hatching of the second-generation eggs, which was the highest in the 10-year period. 1948, however, was highest in first-generation egg hatching and second-generation larval maturing and lowest in second-

generation egg hatching. These facts suggest that the success of the development of one stage was not associated with that of other stages during the same year. This may be explained first, by the fact that the requirements for the successful development of different stages, both physical and biotic, are very different.

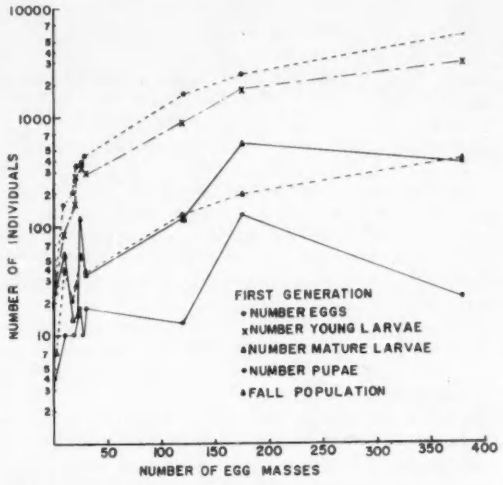


FIG. 2.—Relation between the first-generation egg-mass population and the populations of the subsequent stages.

Thus Kozhantshikov (1938) showed differences in the optimal temperatures and humidity for the various stages of borer development. Stirrett (1938) showed that the optimal temperature for the adult flight was in the narrow range of 18.4° to 21.1° C. The different habitats on the corn plant of the different stages of corn borer, and the different feeding sites of the different larval instars have been shown by many workers. Furthermore, the different stages of the borer life cycle are exposed to quite different types of hazards, as suggested by the diversity of factors which adversely affect borer populations (Barber 1926, Stirrett 1938, and Chiang 1959).

A second point is of equal importance. Even if the requirements for the successful development of successive stages were similar, the environmental conditions usually change so rapidly that different stages will be exposed to very different conditions. Kozhantshikov (1938) showed that the optimal temperature of the different instars of borer larvae is between a reasonably confined range of 25° to 30° C. But in southern Minnesota, the day-to-day variations in temperature sometimes are so great that one larval instar may be exposed to the optimal temperature range while the next instar may be exposed to a temperature much above or much below the optimum.

The present results may be compared with Stirrett's results (1938) in Ontario from 1928 to 1936. He found that five of these years showed an increase over the preceding years, and three showed a decrease. He checked the biological events which brought about the final populations. His results are condensed and presented in table 4. These results also show that the degree of success of the development of one stage is independent of the success of other stages. Also of interest is the fact that no two of the eight years had the same pattern. This indicates that the determining environmental factors were not the same in different years.

Figure 4 also reveals the comparative variability of the three biological events, the maturing of first- and second-generation larvae, and summer pupation. With few exceptions, the maturing of the first-generation larvae during the 10-year period varied between 10 and 14 percent, and the maturing of the second-generation larvae, between 0 and 10 percent. In both cases, the degree of success was rather low, and the variability was small. Pupation, however, varied from almost 0 to 100 percent during the same period.

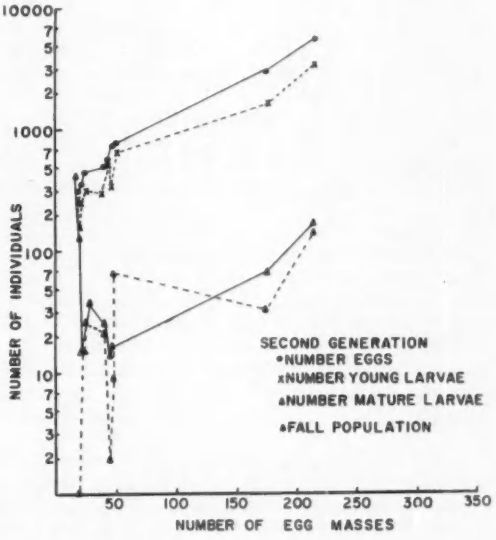


FIG. 3.—Relation between the second-generation egg-mass population and the populations of the subsequent stages.

The low degree of success of corn-borer larval development has been termed by Thompson and Parker (1928) as an "intrinsic controlling factor". They reported a considerable mortality among the young larvae even under ideal conditions. This fact, observed by other workers also, will explain the generally low larval survival. The even

Table 2.—Population levels of various stages for each of the 10 years expressed in terms of an initial density of 1000 eggs.

Year	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957
First generation										
Eggs	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
Young larvae	858	624	509	527	560	642	818	——	750	1000
Mature larvae	150	63	75	108	272	87	103	——	74	250
Pupae	26	58	4	10	66	42	49	——	51	143
Second generation										
Eggs	1000	1000	1000	1000	1000	1000	1000	1000	1000	1000
Young larvae	432	647	914	528	525	646	912	680	863	560
Mature larvae	84	27	0	0	11	5	4	46	12	42

lower success of the second generation needs a further remark. Without venturing into detailed analyses of individual factors, it suffices to say that in southern Minnesota frosts come early relative to borer development during the later part of the growing season. The frost may either be severe enough to kill the immature larvae directly or may merely kill the corn plant, which will dry out and become unsuitable as food. In either case, many borers die of frost or starvation before they reach maturity for overwintering.

The second point is relative to the high variability of the percent of summer pupation in contrast to the restricted variability of the success of larval development. Morris (1957) stated that variable mortality factors may have more influence on population fluctuations than constant mortality factors. Similar reasoning can be applied here. Larval mortalities were high in all years, and were responsible for the generally low levels of population in the area. The percent of pupation, however, was greatly variable from year to year, and hence could have been important in causing fluctuations. As will be discussed in a later section, the percent of pupation is a pivotal point in determining the size of the second-generation population and the direction and magnitude of the year-to-year population fluctuations.

To summarize this aspect of the population dynamics, the following points may be made:

(1) The success of the development of one stage is independent of the success of other stages during the same generation in a given year.

(2) For this reason, the borer populations of different stages fluctuate in a random fashion.

(3) The random fluctuations may be attributed to the varied requirements of the different life stages and to fluctuating environmental conditions.

(4) Young larvae suffer a heavy mortality even under the most favorable conditions. For this reason, while the remaining population may be quite sensitive to environmental conditions the chance of many larvae reaching maturity remains consistently low.

Table 3.—Survival of various stages of the European corn borer in Waseca, Minnesota. 1948–1957.

Year	1948	1949	1950	1951	1952	1953	1954	1955	1956	1957	Mean	Coef. var. (%)
First generation												
Aver. number of eggs per mass	14.6	13.8	15.3	14.5	13.7	16.0	10.7	——	17.1	11.2	14.1± 2.1	14.9
% Eggs hatched	85.8	62.4	51.3	52.7	56.3	64.1	81.8	——	74.7	100	69.9±17.9	25.6
% Larvae matured	17.4	10.0	14.6	14.6	48.2	13.6	12.6	——	10.0	25.0	17.4±10.4	60.0
% Mature larvae pupated	17.5	92.0	5.5	9.6	24.4	48.7	47.6	100	67.8	57.1	46.9±32.8	70.0
Second generation												
Aver. number of eggs per mass	16.6	23.3	16.1	16.4	17.0	18.4	13.0	15.9	16.6	13.2	16.7± 2.8	16.8
% Eggs hatched	43.2	64.7	91.4	52.8	52.5	64.6	91.2	68.0	86.3	56.0	68.9±17.8	25.8
% Larvae matured	19.5	4.2	0	0	2.2	7.8	3.8	6.7	1.3	7.5	6.6± 5.6	89.4
Fall population												
% First generation	42.3	8.1	100	100	42.5	38.8	84.8	0	50.8	14.0	48.1±36.3	75.4
% Second generation	57.7	91.9	0	0	57.5	61.2	15.2	100	49.2	86.0	51.9±36.4	70.1

(5) Summer pupation showed the greatest variability, and might be expected to be a more important determinant of the direction and magnitude of the fluctuations of borer populations than the larval mortality which was consistently high.

POPULATION CHANGES AMONG THE TWO GENERATIONS OF THE SAME YEAR

The numbers of individuals of the same stages of the two generations varied greatly in the same year. Table 1 shows that the egg population of the second generation was higher than that of the first generation in some years (slightly higher in 1953, doubled in 1948, 1949, and 1956, tripled in 1954, and more than 15-fold in 1952, 1955, and 1957) and lower in others (1950 and 1951). Similarly, great variations were shown in the number of young and mature larval populations of the two generations. Of particular interest is the comparison of the changes of the number of first-generation mature larvae, the number of mature second-generation larvae, and the mature larval population in the fall. The three sets of numbers, as shown in table 1, seem to vary independently. Furthermore, as shown in table 3, the percent of the fall population contributed by the residual first-generation larvae again varied greatly. These variations suggest a complex nature for the quantitative relationship between the first-generation borers, the second-generation borers and the fall population. An attempt is made to analyze these relationships on the basis of the 10 years' data.

To facilitate the discussion, pertinent data are extracted from tables 1 and 3, and are presented in table 5. Items 1, 3, 4, and 5 are transcribed from table 1, items 2 and 6 from table 3, and items 8, 9, 10 and 11 are recalculations made on the assumption of there being 100 mature larvae each year at the end of the first generation (item 7).

Item 12 is the percent ratio of the calculated number of mature second generation borers to the numbers of pupae produced in midsummer (item 10/item 8). This ratio has been termed by Balch and Bird (1944) the "index of population trend". It is apparent that the I.P.T. reflects the favorability of environmental conditions for the development of the second generation. The highest I.P.T. during the 10-year period was 640 (1948), which means that when the conditions are favorable there may be as many as seven second-generation larvae reaching maturity during the fall for every first-generation larva which pupated during the summer. In most of the years, however, the conditions were much less favorable, hence the I.P.T. values were much smaller. In 1950 and 1951, early frosts killed all the second-generation larvae before they reached maturity, and hence the indices were 0. Although the index never exceeded 700 in this study, it is realized that it could be higher if a given field attracted a large number of moths from the adjacent fields because of differences in the growth of the plants. Increases higher than sevenfold have been mentioned in informal reports made by workers in other states.

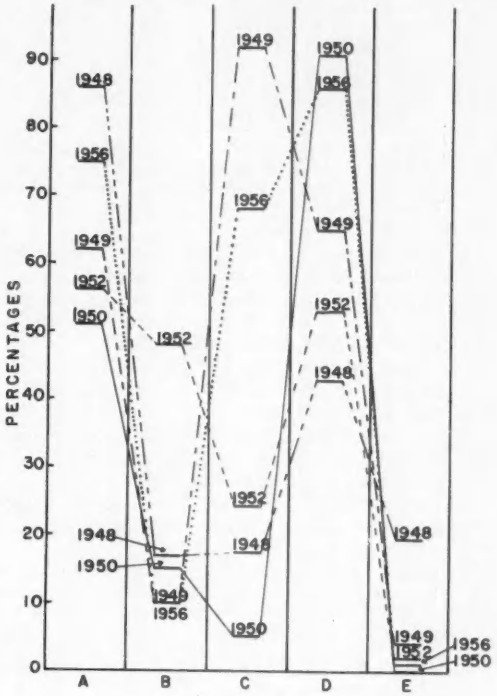


FIG. 4.—Variation of the degree of success of various events: A, First-generation hatching; B, First-generation larvae maturing; C, First-generation pupating; D, Second-generation hatching; E, Second-generation maturing.

It should be understood that this index is computed on the basis of the number of first-generation pupae and the number of second-generation mature larvae, and is merely a description of the events after they took place. And, while it helps to analyze and understand the basic characteristics of the population changes which took place, it is not an evaluation of the effectiveness of particular environmental factors. Therefore it does not aid in predicting population changes.

The significant aspects of the relationships between the first-generation, the second-generation, and the fall populations are also schematically depicted in figure 5. In order to bring together the interrelationships of several factors, the diagram is constructed by superimposing one graph on another. Because of the complexity of the graph, some detailed explanation will be given.

Table 4.—Population changes of the European corn borer in Ontario.[a]

Comparison	Moth population	Fecundity	Egg survival	Larval survival	Overall changes
1929 compared to 1928	− − −	+ + +	−	− −	− − −
1930 compared to 1929	+	+	same	− −	− −
1931 compared to 1930	− −	−	same	+ + +	+ +
1932 compared to 1931	+ +	+	− −	− − −	+
1933 compared to 1932	+	−	+	−	+
1934 compared to 1933	− − −	+	−	+	− − −
1935 compared to 1934	same	+	+	+	+ +
1936 compared to 1935	+ + +	−	+	−	+ +

[a]Results condensed from Stirrett's data (Stirrett 1938, Tables 2–9). +indicates some increase, ++double, +++triple or more, −decrease, −−decreased to less than half, −−−decrease to less than one-third.

In this diagram the vertical scale on the left (a-e) represents the number of mature borers in the field in the fall, calculated on the basis of 100 mature larvae at mid-summer (item 7, table 5). A fall population at the level of point c on this scale indicates that there has been no numerical change in the population from midsummer to fall. Fall populations which lie above or below point c indicate either an increase or a decrease from the number of larvae present at midsummer.

The percent of pupation has varied in different instances (item 6, table 5). The possible range of variation, 0 to 100, is indicated on the abscissa (a-b), and is represented by the stippled triangle (c-b-d). The percent of first-generation mature borers which did not pupate and remained to be counted in the fall constitutes the residual first-generation larval population, and is indicated in the graph by the hatched area (item 9, table 5). Any pupation during midsummer will reduce the number of mature first-generation larvae. Thus the hatched area decreases as the amount of summer pupation increases from (a) to (b).

The scale on the right (b-f) is the index of population trend (I.P.T.) which, as mentioned earlier, reflects the degree of favorability of

Table 5.—Relation between first-generation mature larval population, summer pupation, second-generation larval population, and mature larval population in the fall.

Year	1948	1949	1950	1952	1952	1953	1954	1955[a]	1956	1957
(1) Number of 1st-gen. mat. larvae	57	150	134	135	41	39	21	0	28	7.5
(2) % pupation	17.5	92.0	5.5	9.6	24.4	47.6	47.6	100	67.8	57.1
(3) Number of pupae	10	138	24	13	10	19	10	——	19	4
(4) Number of 2nd-gen. mat. larvae	64	36	0	0	34	24	2	16	9	21.5
(5) Number of mature larvae in the fall	111	147	410	122	59	39	13	16	18	25
(6) % 1st-gen. larvae in the fall population	42.3	8.1	100	100	42.5	38.8	84.8	0	50.8	14.0
(7) Number of 1st-gen. mature larvae	100	100	100	100	100	100	100	100	100	100
(8) Number of pupae	17.5	92	5.5	8.7	24.4	48.7	47.6	——	66.7	53.3
(9) Number of 1st-gen. residual larvae	82.5	8	94.5	91.3	75.6	38.5[b]	52.4	0	32.3	46.7
(10) Number of 2nd-gen. mature larvae	112.3	90.7	0	0	82.9	61.5	9.5	——	32.1	286.7
(11) Number of mature larvae in the fall	195	98.0	94.5	90.4	158.5	100	61.9	——	64.3	333.3
(12) Index of population trend $(\frac{(10)}{(8)} \times 100)$	640.0	99	0	0	340	126	20	——	47	537

[a]In 1955 there were no first-generation egg masses, larvae, or pupae on the plants marked and checked for the study. Some found elsewhere in the same field showed 100 percent pupation, and 16 second-generation larvae matured on the marked plants.

[b]If all first-generation larvae had survived, the number of first-generation residual larvae would have been 51.3 instead of 38.5.

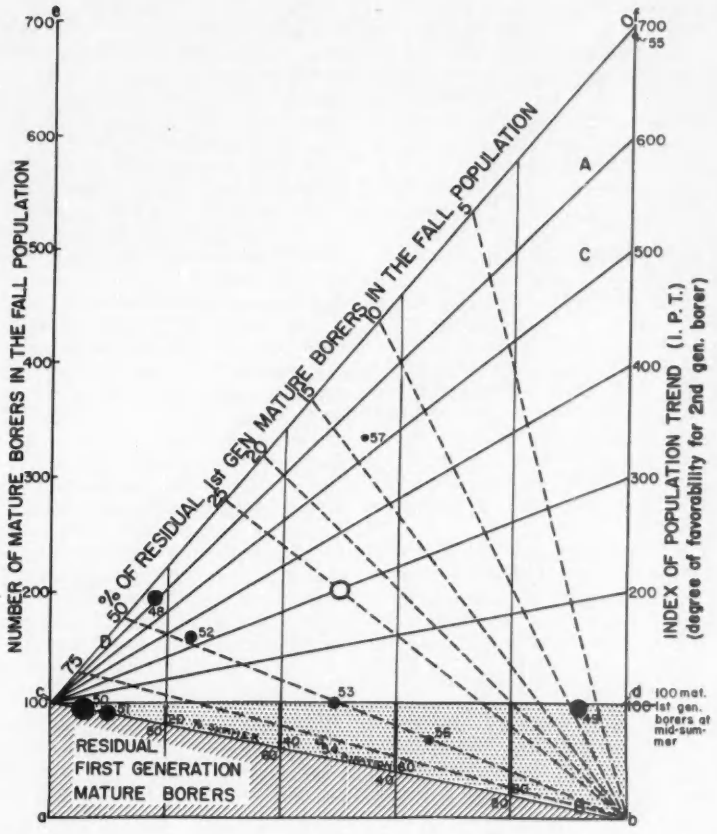


FIG. 5.—Relation between the first-generation and the second-generation larval populations, when the first-generation larval population is 100. (See explanation in text.)

environmental conditions for the second generation (item 12, table 5). I.P.T. values above (d) indicate some degree of population increase in the second generation over the number of pupae at midsummer, while values below (d) indicate a net loss.

At first glance, the scales on the two ordinates may seem to duplicate one another. They both indicate population changes. However, the one on the left (a-e) indicates the total fall population, including both first- and second-generation larvae, while the one on the right (b-f) is an index of the degree of success of the second-generation population.

The oblique lines running radially from (c) to vertical line (b-f) represent different I.P.T. values, i.e., different degrees of favorability for the second generation. The positions where these oblique lines intersect a vertical line corresponding to any percentage of summer pupation indicate the possible population increase allowed by various degrees of I.P.T. For example, the point which represents a 50 percent pupation and an I.P.T. value of 300, as shown by the circle (in the middle of the graph), if projected to the line a-e, will indicate a fall population of 200 larvae. This means that with this combination, there would be a two-fold increase from 100 in the midsummer to 200 in the fall. With other combinations it is possible to find as few as 0 or as many as 700 mature larvae in the fall.

The second set of oblique lines (dashed) running radially between point (b) and diagonal line (e-f) indicate the percent of residual first-generation mature larvae in the fall population. For example, with a fall population of 200 and with an I.P.T. of 300, as given in the previous example, the circled point falls on the dashed oblique line which indicates that 25 percent of the fall population consists of residual first-generation mature larvae. This would be the case because in this example 50 of the 200 larvae were from the first

generation and 150 were from the second generation. If 100 percent of the summer population had pupated, no residual first-generation larvae would be found in the fall population, regardless of the size of the fall population. This situation is represented by the vertical scale on the right which coincides with the 0 line for the percent of residual first-generation larvae present in the fall.

The fall populations for the 10 years are then plotted on the diagram. The *size* of the symbol indicates the actual size of the fall population. Thus 1952 and 1953 had 59 and 39 borers in the fall, respectively, and are represented by symbols of similar size, while 1950 had 410 borers in the fall, and is represented by a large symbol. The *position* of the symbol indicates simultaneously (1) the percent of pupation during the summer, (2) the number of larvae in the fall, and (3) the percent of the fall population which is contributed by the residual first-generation borers. These values for the different years are expressed on a common basis of 100 first-generation mature larvae. Some examples will help to illustrate the point.

Table 5 shows that in 1948 the summer population of mature larvae was 57, and the fall population was 111. On the basis of an assumed first-generation population of 100 mature larvae instead of the actual 57, there would be 195 mature larvae in the field. In addition, the summer pupation was 17.5 percent. In figure 5 the sympol for 1948 was placed at a position on their respective scales which fits the values for fall population and summer pupation. And since the actual number of borers in the fall was 111, the symbol is of a median size compared to the symbols for all years. The fact that the symbol is above point (c) on the left ordinate indicates that the fall population was larger than the mature borer population at midsummer, in this case, a two-fold increase.

The location of the symbol for 1949 shows that there was a very high pupation (over 90 percent), a slight decrease in borer population from midsummer to fall (from 100 to 98), and a low percent of first-generation borers in the fall population (less than 10 percent). These values again represent the data given in table 5 for that year.

By projecting these symbols along the oblique lines onto the vertical scale on the right, it may be seen that the symbol for 1948 corresponds to a high index (640) while that for 1949 a much lower index (99). This means that the conditions were much more favorable for the production and maturing of second-generation larvae in 1948 than in 1949.

The symbols for the other years may be interpreted in a similar manner. However, one exceptional point should be clarified. 1955 had no first-generation egg masses, larvae, or pupae on the plants which were marked and checked for these records. The first-generation population in that field was undoubtedly extremely low but by no means absent, since larvae were found later on other plants in the same field. Pupation of these larvae was found to be 100 percent. During the second generation, eggs and larvae were found on the marked plants and 16 larvae reached maturity in the fall. It was inferred that the first-generation population was extremely small and that the 16 mature larvae in the fall, although itself a small number, represented a proportionally large increase. Thus the symbol for 1955 was made very small, but was placed to indicate 100 percent pupation and a near-maximum degree of favorability for the second generation.

The diagrammatic presentation of the quantitative relationships between the mature larvae in midsummer and those in the fall reveals some basic characteristics of the population dynamics of the corn borer in this area. These characteristics are not easily seen by mere examination of the numerical records given in table 5. First, the effects on the fall population of the initial first-generation population, the percent of summer pupation, and the degree of favorability for the second generation are very different. Another characteristic is illustrated by the ranging of the several biological events during the 10-year period over all dimensions of the diagram: the percent of pupation—from about 5 to 100, the percent of residual first-generation borers in the fall population—from 0 to 100, and the degree of favorability for the second generation (I.P.T.)—from 0 to about 700. In other words, the points were scattered throughout the entire triangular area (c-b-f). This fact suggests that the possible types of quantitative relationships between the first-generation, second-generation, and the fall populations are unlimited. With combinations different from those we have observed very different population changes undoubtedly will occur. Some further analyses will help to illustrate the possibilities and limitations.

1. The effect of the initial first-generation population on the fall population.

In 1955 the first-generation population was extremely low. Thus the fall population was quite low in spite of the fact that the percent of pupation and the probable degree of favorability for the second generation were both extremely high. However, had the conditions in the early summer been favorable for moth activity and hence the first-generation egg population had been high (at the level of 1950), the fall population could have soared to an extremely high level. In 1950 the high fall population was due exclusively to the extraordinarily high first-generation population because of the absence of any mature second-generation larvae in the fall. Thus had the first-generation egg population of that year been at a lower level (at the level of 1948) the fall population might have been much lower.

These examples show that, other things being equal, the initial first-generation population may exert a direct effect on the fall population.

2. The effect of percent of pupation on the fall population.

In 1948 the population of mature larvae in the fall was double of that during the midsummer. Had the percent of pupation been as high as in 1949, the fall population could have risen to six times the first-generation population. This hypothetical combination of 1948 and 1949 conditions

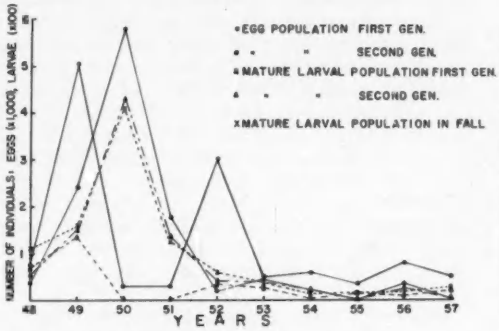


FIG. 6.—Fluctuations of different life stages throughout the 10-year period.

is indicated in the diagram by the position A. On the other hand, in 1950, the fall population was slightly lower than that of the first-generation mature larvae in the midsummer. Had the percent of pupation been increased to the 1949 level, the fall population could have dropped to near zero, as represented by position B in the lower right hand corner of the diagram. These examples illustrate that an increase in the percent of pupation may both increase and decrease the fall population. Under certain conditions, however, a change in the percent of pupation may not change the level of the mature borer population in the fall at all. In 1949 and 1953, the fall population was at about the same level as the first-generation mature larval population at midsummer. Pupation in 1949 was approximately 90 percent while in 1953 it was about 50 percent. Had the percent of pupation for the 2 years been reversed, or changed to any other levels, the size of the fall population could have remained at about the same level. An examination of the diagram will show that the line which represents the I.P.T. of 100 lies horizontally and coincides with the line c-d. The projection of any point on this line to the left hand vertical scale will be 100. This means that with an index of 100, 100 mature larvae in the midsummer will always result in 100 mature larvae in the fall, regardless of the percent of pupation. The degree of favorability in 1949 and 1953 were 99 and 126 respectively, both of which were close to the line for 100. It should be noted, however, that while changes in the percent of pupation would not affect the level of the fall population, they would greatly affect the composition of the fall population. A decrease in pupation would increase the percent of first-generation mature borers in the fall population and an increase in pupation would have a reverse effect.

3. The effect of the favorability of conditions for the second generation (I.P.T.) on the fall population.

In 1949 the population of mature larvae was about the same in the fall as in midsummer. Had the degree of favorability been at the 1957 level, as represented in the diagram by position C, the fall population could have been five times as large as the midsummer population. However, in 1951, the degree of favorability was low (I.P.T. = 0), hence the fall population was slightly lower than the first-generation mature larval population. In this year, even if the I.P.T. had been at the maximum (700) as in 1955, the fall population could never be more than 1½ times that of the first generation. This hypothetical combination of conditions of 1951 and 1955 is indicated in the diagram by the position D. It is evident in the diagram that this low degree of sensitivity of the fall population to changes in the degree of favorability is contingent on a low percent of pupation.

The above discussions disclose certain basic characteristics of the possible quantitative relationships between the borer populations at midsummer and fall. These characteristics may be summarized as follows:

1. A summer population of a given size may give rise to fall populations many times larger, or may result in fall populations a fraction of the original size. The quantitative relationships of the populations of the two seasons during a given year are affected by interactions of (1) the size of the first-generation population, (2) the proportion of the first generation that pupated in the summer, and (3) the favorability of the environment for the second generation. The last factor is perhaps determined by (a) the selection of fields and plants for egg deposition by the second-generation moths, and (b) the mortality of the different developmental stages of the second-generation individuals, especially the frost killing of immature larvae in the fall.

2. Other things being equal, the first-generation population can exert a direct effect on the size of the fall population.

3. At a given percent of pupation, the level of the fall population may be directly affected by the degree of favorability for the second generation as shown by the index of population trend. And, the sensitivity to this effect can increase with the increase in percent of pupation.

4. With the I.P.T. of 100, pupation will have no effect on the size of the fall population. If the index is above 100, the fall population may be directly proportional to pupation, and the proportionality may increase with an increase in pupation. When the index is below 100, the fall population could be inversely proportional to pupation. Again, this inverse proportionality may increase with an increase in pupation.

5. Fall populations of the same size may consist of very different proportions of residual first-generation larvae and second-generation larvae. Other things being equal, the percent of first-generation larvae in the fall population is likely to be inversely proportional to the percent of summer pupation.

6. It is apparent that in areas where the summer pupation is consistantly complete (100 percent), the population in the fall will be simply proportional to the degree of favorability for the second generation and will consist of second-generation larvae exclusively. This simple relationship is represented in the diagram by the right hand vertical scale (b-f).

POPULATION CHANGES DURING THE 10-YEAR PERIOD

As far as the year-to-year fluctuations of borer populations are concerned, more emphasis has been given in the literature to the population of the mature larvae in the fall than to that of other stages. This is perhaps because (1) the population in the fall represents the most stable life stage, (2) it is present in both one-generation areas and multigeneration areas, (3) it is considered as a basis for estimating the loss in yield of corn due to borer infestation in the current year, and (4) it is believed to indicate the potential level of borer infestation the following year. For these reasons, statewide and countrywide surveys of borer populations are made in the fall.

In the present study, equal emphasis is given to all the stages which are present in the growing season. Figure 6 shows the fluctuations of the different life stages throughout the 10-year period. It is to be noted that the graphs of egg populations and the larval populations are on different scales. The graphs show that during the 10-year period different life stages showed different numbers of peaks, and that even the prominent peaks varied in number. Furthermore, the prominent peaks for the different stages occurred in different years.

The first-generation egg population showed three peaks, 1950, 1953, and 1956, with a prominent peak in 1950, while the second-generation egg population showed four peaks, 1949, 1952, 1954, and 1956, with the first two both prominent. The fluctuations of the populations of the young larvae followed the same trends as the egg populations. The first-generation mature larvae showed a prominent peak in 1950 and a small peak in 1956. The second-generation mature larvae showed three peaks, 1949, 1952, and 1955. The first of these may be considered prominent, but was still on a much smaller scale than the prominent peaks in other stages. The fall population of mature larvae reached a prominent peak in 1950 and fell off progressively to the lowest level in 1954, and, up to 1957, was on a gradual increase.

The above facts suggest that no single life stage is representative of the borer population fluctuation in Waseca during the 10-years under study, and that the interval between peaks of the fluctuations, if a mean value of this is to be sought, will not be the same for all life stages.

The fluctuations of the fall populations during the 10 years are analyzed from another approach, namely, whether the peaks have taken place in the same years in Waseca as in other localities. Two other studies have been published which were carried out in the north-central region and which covered similar periods. Although the results of the present study were from one field in Waseca, Minnesota, while the other studies were on the basis of state averages, certain significant aspects of the borer population dynamics can be elucidated by the comparison of the three studies. The fluctuations are shown in figure 7.

The graphs show that during the years covered by both Illinois (Bigger and Petty 1953) and Ohio (Neiswander 1952) the fluctuations followed about the same pattern, with the exception that Ohio showed a peak in 1943 which was not shown for Illinois. The graphs also show that there were only 4 years (1948 to 1951) which were covered by all three states. By coincidence, this period included the most prominent peak of the fall populations during recent years. Of fundamental importance is the fact that the peak took place in 1949 in Illinois and Ohio, but in 1950 in Waseca, Minnesota. Examination of the records of fall populations alone could easily lead to an interpretation of this difference as a lag of one year in the buildup of the populations in Waseca as compared to those in Illinois and Ohio. But information on the population changes which took place prior to and resulted in the fall populations in Illinois and Waseca suggest that this lack of synchronization resulted from a higher fall mortality in 1949 in Waseca than in Illinois, and a higher summer pupation in 1950 in Illinois than in Waseca. Thus the mechanisms which brought about the peaks in different years were different and were independent of each other.

Referring to the previous section (see tables 1 and 3, and also figure 5), records in Waseca in 1949 show that the second-generation egg and young larval populations were extremely high, but the survival of the larvae during the fall was very low (4.2 percent). This, coupled with a small residual first-generation larval population as a result of a high summer pupation (92.0 percent), the fall population became very small in comparison with the populations of the earlier stages. In contrast,

the survival of the larvae in the fall in Illinois was above the average for that area, (Bigger and Petty 1953). This high survival resulted in the unusually high larval population in the fall. The seasonal changes in population in Illinois in 1944 were very similar to the hypothetical situation indicated by position C in figure 5.

Regarding the 1950 populations, the survival of first-generation eggs and larvae was extremely high in Waseca, but the fall conditions were such that the second-generation larval survival was nil. Thus the fall population consisted exclusively of residual first-generation larvae. The summer pupation was extremely low (5.5 percent) in that year, and 94.5 percent of the first-generation mature larvae remained as larvae. Since the initial number of first-generation larvae was high, the residual population constituted the highest fall population in the 10-year period even in the complete absence of second-generation larvae. In other words, with the fall conditions as they were, the low summer pupation actually conserved the population. It was postulated that had the summer pupation in 1950 been high, the fall population of that year would have been much lower. Apparently this was what had taken place in Illinois in 1950. Bigger and Petty (1953) observed in Illinois that borer numbers in 1950 were greatly reduced during the summer months (no figures given). This reduction suggests a high summer pupation. They further reported that large numbers of borers were immature during the fall of 1950, hence the reduction of living borers during the fall and winter was the highest (89 percent) during the 10-year period studied. Thus the population changes which took place in Illinois in 1950 were very similar to the hypothetical situation represented by position B in figure 5, and resulted in a low fall population.

This discussion elucidates the possible mechanisms involved in the lack of synchronization in the prominent peaks in the fall population between Waseca and Illinois. Although published information regarding the population changes in Ohio does not contain the needed details, it is probable that the same mechanisms were involved. The facts presented suggest that peaks may not always take place in the same year in different localities. These facts confirm Cole's conclusion (1954) that "Meterological phenomena doubtless underlie many of the population fluctuations and it is conceivable that the influence of such factors may sometimes be sufficiently widespread to keep the cycle fairly well synchronized over large areas. However the diversity of haphazard influence to which populations are subject lead us to suspect that the resultant fluctuations would occur essentially at random . . .". These facts support the conclusion that the haphazard variations of the environment may induce unlimited numbers of patterns of seasonal changes of borer populations.

Another point might be mentioned in this connection. The occurrence of prominent peaks in Ohio in 1940 and 1949 may easily lead to some expectation of a classical oscillation of 9-10-year intervals. Since it is shown that peaks resulted from a series of coincidental and independent events like those which took place in Illinois in 1949 and in Waseca in 1950, it is doubtful that the peaks will recur at 9-10-year or any regular intervals more often than by chance. Long-term studies are needed to verify this contention.

Among the reasons for using the number of mature larvae in the fall as the representation of the borer population in a given locality, as enumerated earlier, the last two must be considered unacceptable. One of these is the value of this number in estimating the reduction in yield of corn. Detailed studies on this aspect have been published elsewhere (Chiang and Hodson 1950, Chiang et al. 1954). The other aspect is that the fall population of one year is indicative of the potential level of borer population in the next season. In order to determine if this has been true in Waseca, figure 8 was con-

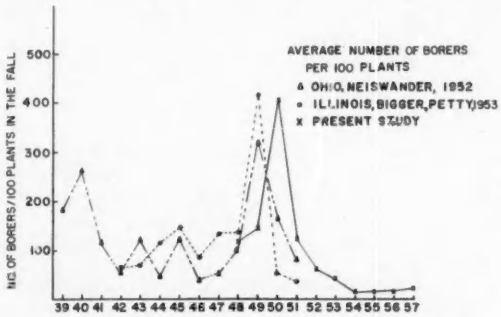

AVERAGE NUMBER OF BORERS
PER 100 PLANTS
▲ OHIO, NEISWANDER, 1952
• ILLINOIS, BIGGER, PETTY, 1953
x PRESENT STUDY
NO. OF BORERS/100 PLANTS IN THE FALL
500
400
300
200
100
39 40 41 42 43 44 45 46 47 48 49 50 51 52 53 54 55 56 57

FIG. 7.—Fluctuations of the fall populations in three localities: Ohio, Illinois, and Waseca, Minnesota.

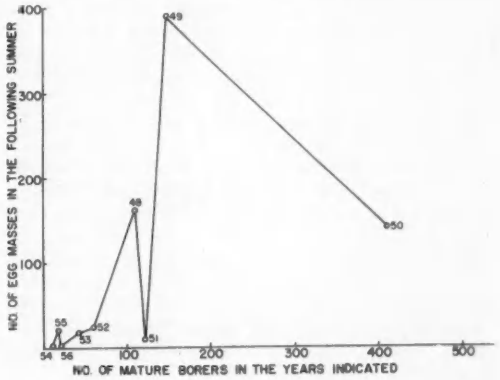


FIG. 8.—Relation between the fall population and the egg population of the following summer.

structed to show the relation between the levels of the two populations. The distribution shows that the egg population of one year was only poorly correlated with the number of mature larvae in the previous fall, particularly in those cases where the fall larval population was in excess of 100 borers per 100 stalks. There were cases where fall populations of similar levels were followed by egg populations of very different sizes. The most striking example is the comparison of records of 1948–49 and 1951–52. Although the causes of the poor correlation were not explored in this study, it may be explained as follows.

As presented earlier, the serial correlations between any two successive stages during the growing season were poor, even though two successive stages involve only one biological event. The sequence between the fall larval population and the spring egg populations, however, involves at least three events: (1) the survival of the larvae throughout the winter, (2) the success of pupation during the spring, (3) the survival, activity, and fecundity of the moths. A good serial correlation would require that the success of each of these events is held at a constant level throughout the 10-year period. Variations in the success of any one of these events may result in a poor correlation as recorded. Bigger and Petty (1953) showed that the factor of larval survival alone varied from 10 to 44 percent during a 5-year period in Illinois. This observation seems to support the explanation offered. The data in fig. 8 also suggest that there may be a fall population level below which a high egg population the following summer will not occur. The grouping of low egg mass numbers for the years 1952–1956, when the previous fall larval population fell much below 100 larvae per 100 stalks, suggests this possibility.

In connection with the serial correlation of population levels of successive years, the theory of random fluctuation as elaborately discussed by Cole (1954) may be cited. He concluded that the populations of successive years cannot be entirely independent, hence populations will depart slightly from complete randomness. From this it may be inferred that the less dependent the populations of successive years are, the more random will be the fluctuations. In the case of the corn borer, the life stages are particularly vulnerable to environmental factors which change constantly and haphazardly. Therefore the degree of dependency shown by populations of successive years is very slight, and hence the population fluctuations show a high degree of randomness.

The discussion in this section reveals the following characteristics of borer population changes during the 10-year period.

1. The fluctuations of the populations of different life stages followed different patterns, hence the mean interval between two successive peaks of abundance was not the same for all life stages.

2. The peaks of the fluctuation of the fall population did not always take place in the same year in different localities. This was the result of independent localized and haphazard changes of the environment. For the same reason, it is not likely that the fall population peaks will recur at any regular intervals.

3. The spring population of one year was only poorly correlated with the fall population of the year before.

DISCUSSION

Recently Milne (1957a, 1957b) has advanced a theory of natural control of insect populations. According to his conception of this somewhat controversial subject, the one true density-dependent factor is competition within the population for food, space, etc. He considers interspecific competition for the same resources and natural enemies to be examples of imperfectly density independent factors. The remaining factors, designated as density-independent, are mainly the elements of weather. While this interpretation of environmental influence on populations is not acceptable to everyone, it will be used as a frame of reference for a discussion of the corn borer population dynamics that we have presented.

In the vast literature on the European corn borer there is no evidence presented of intra- or interspecific competition for resources. Instead, some recent work suggests that intraspecific competition is quite unlikely to be a limiting factor in the population growth of this species, at least at the population levels observed in the present study. When Everett et al. (1958) artificially infested corn plants with three and six egg masses per plant they found a significantly larger number of larvae established in the plants that received six egg masses (approximately 120 eggs per plant). This means that there could be a larger population increase with over 10,000 eggs deposited per 100 plants than at the lower rate of about 6,000 (three egg masses per plant). Since even the lower rate of 6,000 eggs per 100 plants was greater than the highest natural population recorded during our 10-year study, there is little evidence for considering competition within the population as a limiting factor at these levels of egg-mass abundance.

The sudden drop in the corn borer population in 1951, following the high peak of abundance in 1950, was due to the combination of low pupation during the summer and poor larval survival in the fall of 1951 rather than to any competitive mechanism.

With regard to natural enemies, considered by Milne to be imperfectly density-dependent factors, little can be said. A considerable number of predators and parasites have been observed

and the effects of some evaluated by Baker et al. (1949) and Chiang and Holdaway (1955). But none of the evidence obtained suggests that these natural enemies have had a determining influence on the pattern of corn-borer population fluctuations. In fact, the fluctuations that we have observed have been random in nature rather than approaching "classical oscillations" that might be expected were natural enemies of major importance.

The other major category included in Milne's theory, the density-independent factors, consists mainly of the elements of weather. Many authors have emphasized the importance of weather on the various stages of the corn borer life cycle. Stirrett (1938) stressed that the temperature influence on moth flight and oviposition and the hazardous effects of heavy rains and high wind on moth activity. He also mentioned that alternating high and low temperature increased egg mortality. Chiang and Hodson (1959) have shown that the percentage of summer pupation is correlated with the accumulation of day-degrees over 50° F. during the development of first-generation larvae. In a previous section it was mentioned that early frost during the fall may prevent second-generation larvae from reaching maturity. Thus it becomes apparent that weather changes, however momentary, if they occur at a critical time, may profoundly affect the activity and survival of the European corn borer. Such momentary changes in weather, which occurred independently and haphazardly during the 10 years of this study, we consider to be the principal cause of population fluctuations within a given year and from year to year.

A number of authors have suggested an important role for the element of chance in the control of insect populations. Thompson (1956) concluded that animals move through a network of random events, events attributable to what is called chance. In his opening address at the Cold Spring Harbor Symposium on Population Studies, Cole (1957) stated that in nature all of the factors making for population changes are interacting in complex ways and random components are brought into the system through the vagaries of weather. He contended further that the effects of such interacting components will result in fluctuation consistant with random variation. More recently Schwerdtfeger (1958) has expressed the opinion that random influences can maintain abundance for as long as a decade. On theoretical grounds he concludes that certain mechanisms may have to intervene as a safety device when the play of chance becomes too one-sided.

The fluctuations of European corn borer populations recorded from 1948 through 1957 at Waseca, Minnesota, are in conformity with the views on the role of chanc eexpressed by these authors.

The fact that during most of the years under observation the borer populations fluctuated at low levels, much below the carrying capacity of the environment, suggests one or both of two things:

1. An intrinsic weakness of the species. As pointed out earlier and also by Thompson and Parker (1928), a large proportion of the young larvae die even under the best conditions. Also, there was a mortality of at least 10 to 15 percent among the eggs throughout the 10-year period. The only exception was the 100 percent hatch recorded for the first generation in 1957.

2. A high degree of vulnerability of other stages to the vagaries of weather. This is suggested by the highly variable rates of summer pupation and of maturity among second-generation larvae.

This vulnerability of the European corn borer may also be considered as evidence of the harshness of the physical environment. Waseca, in contrast to the southern portion of the corn belt, has generally lower minimum temperatures. Such temperature extremes are responsible for retarding larval growth and reducing pupation during the growing season, and killing the host plants or immature larvae toward the end of the season. Andrewartha and Birch (1954) concluded that populations at the fringe of the distribution of the species often are exposed to harsh physical conditions and may as the result fluctuate at low population levels. The European corn borer in the southern Minnesota area may be considered to be an example of such a fringe population.

The European corn borer first appeared in significant numbers in Minnesota in 1947. Detailed records of population changes have been maintained since 1948, and the analyses of a 10-year record have shown that the borer population in this area have fluctuated at a low level in a random fashion. As mentioned above, these characteristics suggest that the borer is at the fringe of its distribution in the area studied, and that the harsh physical conditions of the environment are principally responsible for its population fluctuations. Under such conditions the pressure of natural selection may be expected to be severe, hence there is the probability of the initiation of adaptive evolution. Continuance of records of abundance, such as those reported here, will be necessary to obtain information on whether or not adaptive evolution is taking place, and its effect, if any, on the population dynamics of this species. Therefore the European corn borer populations in southern Minnesota present a challenge as well as an opportunity to investigate the long-term population trends of an insect since its establishment in a new and fringe area.

REFERENCES CITED

Andrewartha, H. G., and **C. L. Birch.** 1954. The Distribution and Abundance of Animals. University of Chicago Press. 782 pp.

Baker, W. A., W. G. Bradley, and **C. A. Clark.** 1949. Biological control of the European corn borer in the United States. U. S. Dept. Agric. Tech. Bull. 983.

Balch, R. E., and **F. T. Bird.** 1944. A disease of the European spruce sawfly, *Gilpinia hercyniae* (Htg.) and its place in natural control. Sci. Agric., Ottawa, 25: 65–80.

Barber, G. W. 1926. The factors responsible for the decrease of the European corn borer in New England during 1923 and 1924. Ecology 7: 142–62.

Bigger, J. H., and **H. B. Petty.** 1953. Reduction of corn borer numbers from October to June. A ten-year study. Illinois Agric. Expt. Sta. Bull. 566.

Chiang, H. C. 1959. A note on some mortality factors of the European corn borer, *Pyrausta nubilalis*. Ecology 40: 310–12.

Chiang, H. C., L. K. Cutkomp, and **A. C. Hodson.** 1954. The effect of second generation corn borer on field corn. Jour. Econ. Ent. 47: 1015–20.

Chiang, H. C., and **A. C. Hodson.** 1950. Stalk breakage caused by European corn borer and its effect on the harvesting of field corn. Jour. Econ. Ent. 43: 415–22.

1952. Relation between egg mass abundance and fall populations of first-generation corn borer and justification for insecticidal control in field corn. Jour. Econ. Ent. 45: 320–3.

1959. Summer pupation of the European corn borer and the seasonal temperature. Jour. Econ. Ent. 52: 409–11.

Chiang, H. C., and **F. G. Holdaway.** 1955. Evaluation of predation of the European corn borer. Proc. North-Central Branch Ent. Soc. America 1955: 63–4.

Cole, L. C. 1954. Some features of random population cycles. Jour. Wildlife Management 18: 2–24.

1957. Sketches of general and comparative demography. Cold Spring Harbor Symposium on Quantitative Biology 22: 253–71.

Everett, T. R., H. C. Chiang, and **E. T. Hibbs.** 1958. Some factors influencing populations of European corn borer in the North Central States. Minnesota Agric. Expt. Sta. Tech. Bull. 229.

Huber, L. L., C. R. Neiswander, and **R. M. Salter.** 1928. The European corn borer and its environment. Ohio Agric. Expt. Sta. Bull. 429.

Kozhantshikov, I. W. 1938. Geographical distribution and physiological character of *Pyrausta nubilalis* Hb. (In Russian, with English summary.) Zoologicheskii Zhurnal [USSR] 17: 246–59.

Milne, A. 1957a. The natural control of insect populations. Canadian Ent. 89: 193–213.

1957b. Theories of natural control of insect populations. Cold Spring Harbor Symposium on Quantitative Biology 22: 253–71.

Morris, R. F. 1957. The interpretation of mortality data in studies on populations. Canadian Ent. 89: 46–69.

Neiswander, C. R. 1952. Fluctuations in corn borer population levels. Proc. North-Central Branch Amer. Assoc. Econ. Ent. 1952: 58–61.

Schwerdtfeger, F. 1958. Is the density of animal populations regulated by mechanisms or by chance? Proc. 10th Internatl. Congr. Ent., Montreal 1956, 4: 115–22.

Stirrett, G. M. 1938. A field study of the flight, oviposition, and establishment period in the life cycle of the European corn borer, *Pyrausta nubilalis* Hbn., and the physical factors affecting them. Sci. Agric., Ottawa, 18: 656–83.

Thompson, W. R. 1956. The fundamental theory of natural and biological control. Ann. Rev. Ent. 1: 379–402.

Thompson, W. R., and **H. L. Parker.** 1928. The European corn borer and its controlling factors in Europe. U. S. Dept. Agric. Tech. Bull. 59.

SOME PIOLOGICAL OBSERVATIONS ON SARCOPHAGA FALCIFORMIS, A PARASITE OF GRASSHOPPERS (DIPTERA: SARCOPHAGIDAE)[1]

WOODROW W. MIDDLEKAUFF
University of California, Berkeley

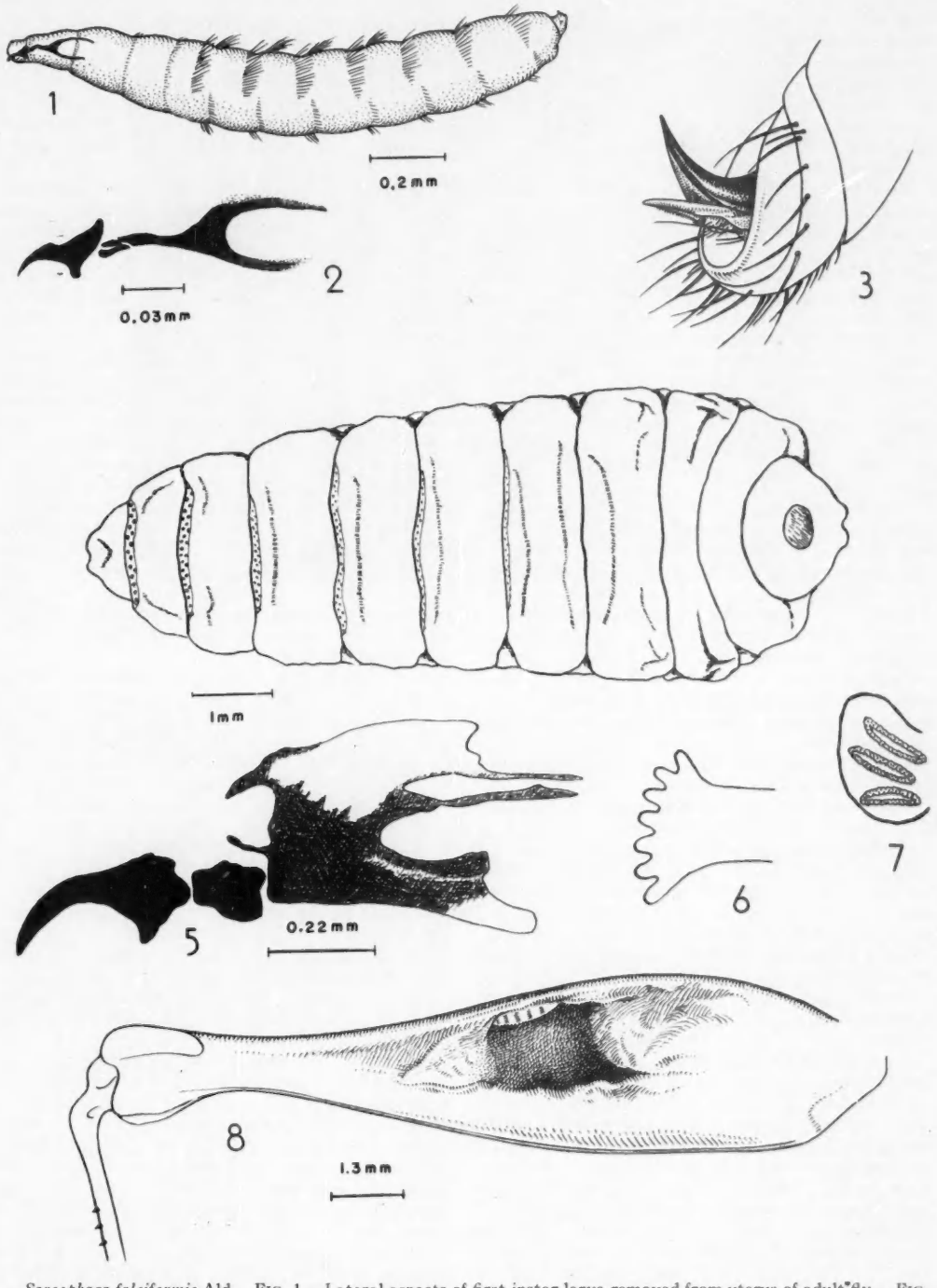
ABSTRACT

S. falciformis Aldrich has been found parasitizing *Melanoplus devastator* (Scudder) and *Oedaleonotus enigma* (Scudder) in California. The female fly viciously attacks adults and older nymphs of these important rangeland grasshoppers, and inserts a larva through the cuticle into the muscles of the hind femur. The larva migrates into the thoracic cavity, where it matures in 6 days. The host dies when the fly emerges, or soon thereafter. The last generation of the flies overwinters as larvae in the soil. *S. falciformis* reduced one localized, heavy population of *M. devastator* almost to the vanishing point.

Periodic outbreaks of rangeland grasshoppers are a common phenomenon in the western United States. At such times parasitism and predation take a concomitant upswing. The serious outbreaks experienced during the 1956 and 1957 seasons were most spectacular in much of California's rangelands. Many thousands of acres supported large populations of *Melanoplus devastator* (Scudder), our most abundant species. Dense swarms moved out of the rangelands into adjacent agricultural areas, causing heavy losses and necessitating the application of insecticides to large areas.

Various authors (Aldrich 1916, Spencer 1958)

[1]These studies were financed in part by funds emanating from Regional Research Project (W-37), a cooperative project with Federal and Experiment Station workers participating in Montana, Colorado, Idaho, Wyoming, and California. Acknowledgment is made to Gerald D. Kelly for help in the field observations and collections, and to Dr. C. W. Sabrosky and Professor H. J. Reinhard for determinations of adult sarcophagids. Accepted for publication March 13, 1959.



Sarcophaga falciformis Ald. FIG. 1.—Lateral aspects of first-instar larva removed from uterus of adult fly. FIG. 2.—Mouthparts of first-instar larvae, lateral aspect. FIG. 3.—Semilateral aspect of female showing tip of abdomen and larvipositor. FIG. 4.—Dorsal view of 5-day-old larva removed from thorax of *Melanoplus devastator* preserved in alcohol. FIG. 5.—Mouthparts of same. FIG. 6.—Anterior spiracle of same. FIG. 7.—Posterior spiracle of same. FIG. 8.—Lateral view of hind femur of *M. devastator*, dissected to show first-instar larva embedded in muscles.

have stated that members of the family Sarcophagidae are the most effective parasites of adult grasshoppers in western rangelands. Just how effective they can be was demonstrated during the 1958 season, when the opportunity to make observations on the bionomics of *Sarcophaga falciformis* Aldrich was presented.

This species was first described by Aldrich (1916) from a male which emerged from *M. devastator* collected at Eureka, California. Subsequent collections and rearings record it from central California and Colorado in the west to South Dakota, Wisconsin and Illinois in the east, and northward into Manitoba and British Columbia.

The first example of parasitism by *S. falciformis* came to our attention on July 18, 1958, in a rangeland area of Alameda County, California, when a single female fly was noted attacking an adult male *Melanoplus devastator*. After the initial attack, which took place on the ground, the grasshopper attempted to escape by flying. The fly followed and appeared to strike the grasshopper in midair, although it was done more rapidly than the eye could follow. The attack was pursued again on the ground when the grasshopper landed. The grasshopper meanwhile trembled spastically, jerking the hind legs, shaking the wings and in a very characteristic manner appeared to be attempting to rub the wings with the hind legs. The tremors subsided in several minutes. The grasshopper was then collected and held alive in the laboratory. Subsequently a mature maggot emerged, pupated, then gave rise to a female *falciformis*.

Several weeks later the area was revisited for further observations and these visits were continued at weekly intervals throughout the remainder of the summer and fall.

A spectacular amount of parasitism was taking place on August 8 and continued at a high tempo until late in September. During the middle of the day, in the warm sunshine, it was not unusual to see 20 or more attacks per hour. The flies made a characteristic buzzing sound which aided in locating incipient attacks. Kelly (1914) reported that a related species *Sarcophaga kellyi* also made a distinctive high-pitched humming noise.

Normally the female of *falciformis* attacked the grasshopper on the ground. Frequently the fly could be seen prior to an attack, sitting on a grass stem, clod of dirt, or other vantage point within several inches of a grasshopper. At the slightest movement she darted upon the prey, time and time again. The grasshopper frantically kicked and flapped its wings, meanwhile attempting to burrow into the duff to escape the attack. This failing, it took to the air, only to be followed by the fly. As many as a dozen flights might be insufficient to lose a persistent and aggressive fly. Occasionally two flies might simultaneously attack the same grasshopper. Several of the larger fifth-instar nymphs were also attacked. Later in the season, when the grasshoppers had become somewhat scarce, attacks could be stimulated by disturbing the grasshoppers and causing them to take to the air, a phenomenon which has been noted by numerous observers with related sarcophagids. For a few moments after a successful attack the grasshopper appeared stunned and might even fall immobile on its side. They could easily be caught with the bare hand during this short period. Grasshoppers were collected immediately following an attack and either placed in alcohol or kept alive for study. Several males and a number of females were reared.

No other insects in the area were observed being attacked or even pursued by *falciformis* females. Several grasshoppers with wings and hind legs removed were thrown in front of female *falciformis*. No more than one quick pass was attempted and then the fly lost interest.

All known sarcophagids which are parasitic on grasshoppers and locusts larviposit externally on the wings or body of the host. Sweetman (1958) correctly deduced that at least some species with a sharp larvipositor place the maggots internally in the host. The method of attack and the manner of larviposition differ appreciably among species and are summarized by Clausen (1940) and Sweetman (op. cit).

Ten wild female flies were dissected and the number of larvae per female counted. They varied from a low of 7 to a high of 47, with an average of 22.1 per female. This is considerably lower than that reported by Clausen (op. cit.) for *Blaesoxipha lineata* which produces a maximum of 285, the highest number recorded for the family. Smith (1940) records an average of 75 and a maximum of 104 larvae for *S. caridei* Brethes, a larviparous species introduced into Canada from Argentina. The low number of larvae produced by *falciformis* is not unexpected for a species which has advanced beyond the more haphazard and risky procedure of placing the larva externally on the host.

Careful examination of grasshoppers, immediately following an attack by *falciformia*, failed to reveal any external evidence of parasitism. The shape and character of the larvipositor of this species (fig. 3) suggested that the larva might be injected directly into some part of the body. A number of grasshoppers were dissected but careful examination of the head, thorax, and abdomen failed to reveal any evidence of parasitism. Since the legs were the only part of the body which had not been dissected, these were then examined. In the sixth specimen opened a living first-instar larva (fig. 1) was discovered deeply embedded in the muscles of the hind femur (figs. 8 and 9). That this is the normal habit for *Sarcophaga falciformis* was subsequently

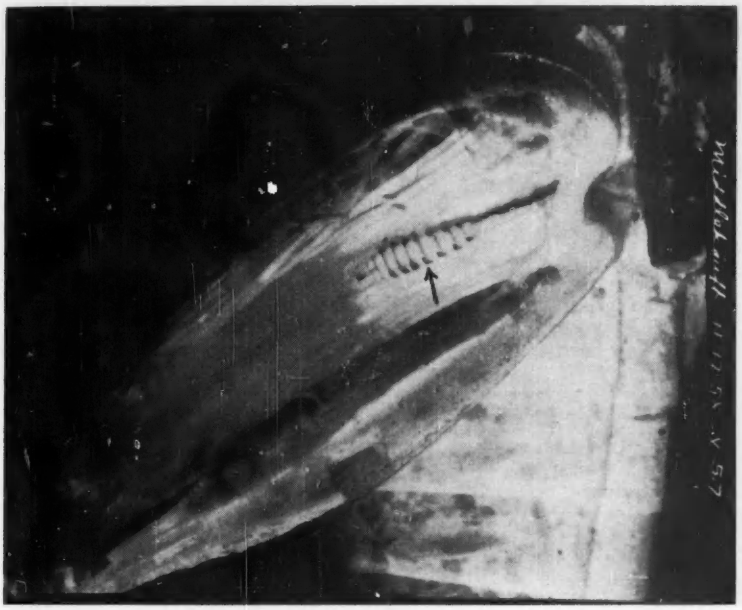


FIG. 9.—Hind femur of *Melanoplus devastator* with cuticle removed, showing first-instar larva of *Sarcophaga falciformis* in situ.

proved by dissecting over 70 specimens of *Melanoplus devastator* and *Oedaleonotus enigma* which had been attacked. These dissections also showed that only 24 percent of the attacks resulted in the deposition of a maggot. In two specimens, however, both femora contained a single larva. The larvipositor is inserted through the heavy cuticle of the femur, leaving no external evidence.

The greatest number of larvae found in the body of a single grasshopper was four. All four emerged on the sixth day following the attack, indicating that they were of the same age.

Several random samples of grasshoppers in the study area were taken and dissected before it was realized that the hind femora should have been examined. Twenty-two percent of the grasshoppers examined contained one or more sarcophagid larvae in their bodies.

This sarcophagid, over a 2-month period, was primarily responsible for wiping out a population of grasshoppers averaging over 20 per square yard when the attacks were first noted. It was not especially difficult to find the hollowed-out bodies of grasshoppers which had been killed by the maggots of this fly.

A number of attacked grasshoppers were held alive in the laboratory, with a few being killed on each day until the sixth day. By the second day following the attack, the larva has migrated into the thoracic cavity. Here and in the abdomen it molts and lives at the expense of the body fat and muscles and other tissues of the host. Parasitized grasshoppers are lethargic and do little feeding in captivity, normally dying when the mature maggot (fig. 4) emerges on the sixth day following the attack. The maggot pupates on the second or third day after emergence, and the imago appears 10 days later. Thus a complete life cycle can take place in 18 days under favorable conditions. There are at least two generations per year, plus a partial third one. The fly overwinters in the larval stage. Several specimens were reared from maggots sifted from the soil in late December 1957.

In one experiment, 8 female *falciformis* were placed in a covered cage, a 1-foot cube, with about 50 *M. devastator* adults. The flies readily attacked, but the grasshopper, upon contact, would jump frantically and slam into the opposite side of the cage, dislodging the fly. Many such attempts to larviposit were noted, but not a single one of them was successful. One fly lived 8 days, feeding avidly upon a solution of honey and yeast.

REFERENCES CITED

Aldrich, J. M. 1916. *Sarcophaga* and Allies in North America. Lafayette, Indiana: Thomas Say Foundation.

Clausen, C. P. 1940. Entomophagous Insects. New York: McGraw-Hill Book Co. (pp. 422–30.)

Kelly, E. O. G. 1914. A new sarcophagid parasite of grasshoppers. Jour. Agric. Res. 2: 435–43.

Smith, C. W. 1940. An exchange of grasshopper parasites between Argentina and Canada with notes on parasitism of native grasshoppers. Ent. Soc. Ontario Ann. Rept. 70: 57–62.

Spencer, G. J. 1958. The natural control complex affecting grasshoppers in the dry belt of British Columbia. Proc. Tenth Internatl. Congr. Ent., Montreal 1956, 4: 497–502.

Sweetman, H. L. 1958. The Principles of Biological Control. Dubuque, Iowa: Wm. C. Brown Co. (pp. 117–9.)

REACTIONS OF SWARMS OF PENTANEURA ASPERA (DIPTERA: TENDIPEDIDAE) TO SOUND[1]

HUBERT FRINGS AND MABLE FRINGS

Pennsylvania State University, University Park, and Mt. Desert Island Biological Lab., Salisbury Cove, Me.

ABSTRACT

Swarms, consisting apparently of males only, respond to simple sounds produced by an audio-oscillator through loud speakers. A startle response occurs when sounds between 80 and 800 cps are broadcast to the swarms at intensities above about 80 db. A second response, an agitated circling and gathering around the sound source, occurs only near 125 and 250 cps, at intensities of 13–18 db. above ambient noise levels for 125 cps, and 3–8 db. for 250 cps. The second reaction, because of its sharply tuned frequency determination and occurrence at remarkably low intensities, could have significance in mating or swarming. The frequency of the male wing sound is about 600 cps, and broadcasts of recorded samples of this to the swarms had no effect. No females were captured at any time; thus the frequency of the female wing sound is unknown. The possible biological significance of the reaction was not determined.

The swarming behavior of small Diptera has been studied by a number of investigators, chiefly with a view to discovering the factors initiating swarming, the stimuli involved in maintenance of the swarm, and the possible significance of the behavior pattern. It seems quite probable that swarms in some manner facilitate reproduction in these flies (Downes 1950, 1955; Gibson 1945), although this may not be true for all species (Nielsen and Greve 1950). It may be that the swarms, which often consist entirely or predominantly of males, attract females visually to the swarms, where they are recognized by the males through their wing sounds. This idea is supported by recent studies on mosquitoes in which it has been shown that males respond with copulatory movements to the wing sounds of females of the species (Roth 1948; Roth and Willis 1952; Tischner 1953; Tischner and Schief 1954). The literature on this subject is reviewed by Roth (1948) and Frings and Frings (1958).

[1]Approved for publication on December 19, 1958, as Paper No. 2329 in the Journal Series of the Pennsylvania Agricultural Experiment Station; supported in part by Research Grant No. E-802 from the National Institutes of Health, U. S. Public Health Service. Dr. Selwyn S. Roback, of the Academy of Natural Sciences of Philadelphia, identified the insects for us, and we are grateful for this. We would also like to express appreciation to James Clegg and Frank Little, students at Penn State, and to Carl Frings for assistance in the field. Accepted for publication March 18, 1959.

The receptors involved in sound-reception in males of the mosquitoes, *Aedes aegypti* (Roth 1948; Tischner and Schief 1954) and *Anopheles subpictus* (Tischner 1953) have been shown experimentally to be the Johnston's organs at the bases of the feathery antennae. These had long been suspected of being receptors for sounds (Johnston 1855; Child 1894a, 1894b; Reibisch 1926; Risler 1953). Downes (1950, 1955) found that the antennal hairs of ceratopogonid males, *Culicoides* spp., were erected when the insects were swarming, but not when at rest, suggesting an involvement of the antennae in swarming behavior. Nielsen and Nielsen (1958) report a similar situation in *Aedes caspius*. The males in swarms may receive sounds and thus be attracted to females entering the swarms. There is no proof, however, that this is the case. In simuliids, on the other hand, Davies and Peterson (1956) found that mating was not facilitated by sounds, but in these insects the antennae are not feathery as in the culicids, ceratopogonids, and tendipedids. The evidence, therefore, is strong for involvement of sounds in the mating of some mosquitoes, but indirect in the case of other small swarming Diptera.

Reibisch (1926), Roth (1948), Roth and Willis (1952), Tischner (1953, 1954, 1955), Tischner and Schief (1954), and Kahn and Offenhauser (1947, 1949) have found that male mosquitoes are

Table 1.—Summary of reactions of swarms of *Pentaneura aspera* to sounds.[a]

Startle				Attraction			
Frequency cps	Reaction	Frequency cps	Reaction	Frequency cps	Reaction	Frequency cps	Reaction
50	0	450	++	Below 100	0	210	0
80	+	500	++	100	0	220	+
100	++	600	+	110	0	230	+
150	++	700	+	120	+	240	++
200	+++	800	+	125	+++	250	++++
250	++++	900	0	130	+	260	++
300	+++	1000	0	140	0	270	+
350	+++	Above 1000	0	140–210	0	280	0
400	++					Above 280[b]	0

[a]The startle reaction is induced by sudden onset of sound and was tested with frequencies at 50 cps intervals below 1,000 cps and at 250 to 500 cps intervals above that. Attraction is obtained with continuous sound and was tested with individual frequencies and with gradually changing frequencies. The reaction units are arbitrary from just perceptible (+) to intense (++++).

[b]Rarely +, at 500 cps.

strongly attracted by sounds produced by females in flight or by artificial sounds at frequencies like those of female wing sounds. Nielsen and Greve (1950) and Nielsen and Nielsen (1958) reported that swarms of *Aedes* spp. were attracted to the investigator in the field by the singing of certain muscial tones. On the other hand, Nielsen and Nielsen (1953) found dispersal of swarms of *Aedes taeniorhynchus* by sounds.

These reports induced us to test the reactions to sounds of swarms of a tendipedid (=chironomid) fly, *Pentaneura aspera* Roback, which is very common at The Mt. Desert Island Biological Laboratory at Salisbury Cove, Maine. The results are reported in this paper.

EXPERIMENTS AND RESULTS

Preliminary observations.—Swarms of *Pentaneura aspera* were found in partly wooded areas and in meadows near the edges of woods almost every fair evening in July and August, when the wind was not too strong. These appeared at about the same light intensity every day and swarmed in groups of a few to about 50 over relatively flat, grassy ground until nearly dark. The reports of Gibson (1945) and Downes (1950, 1955) induced us to try to discover "swarm markers" being used by the insects, but none were obvious. The swarms, however, formed at essentially the same spots every day, and, if blown away by gusts of wind, hurried back to the places. The movements in the swarms were generally of the zigzag type described by Gibson (1945), probably because the swarms were in sheltered areas where there was little wind. Numerous captures by netting have so far yielded no females, so these are male swarms.

By using the voice to produce various musical tones, it was discovered that these insects were very sensitive to sounds. The swarms jumped perceptibly when one emitted a sudden sound in the frequency range, 200 to 500 cps. If one sang a note in this range loudly enough, swarms at distances up to 5 to 8 meters were caused to jump, as if startled. In this case, the individuals apparently all increased their flight speed momentarily, thus giving the impression of jumping by the whole swarm. If one approached a swarm, which usually moved upward as he moved under, and hummed or sang continuously, running up and down the musical scale slowly, he noted that the swarm was relatively unaffected until he reached certain frequencies, whereupon the individuals in the swarm were thrown into agitated circling movements and the swarm descended and formed around his head. By matching the notes found to be most effective against oscillator tones, it was found that they were near 125 and 250 cps.

These observations led to a more exact series of tests, using tones produced by an audio-oscillator (Hewlett-Packard, Model 200A) activating a loud speaker (Jensen, Type NF 101). Two techniques were employed: (1) the sound was turned on suddenly to induce the momentary darting of individuals (startle reaction) in swarms at distances of 1.5 to 2 meters, and (2) continuous tones were broadcast to swarms within about 1 meter of the speaker to attract the swarms to the speaker.

The startle in swarms could be induced by sounds in a wide band of frequencies, about 100 to 700 cps. On the other hand, attraction of the swarms in agitated circling flight around the speaker occurred only at two narrow frequency bands, about 125 and 250 cps. If one changed the frequency from low to high very slowly, with the sound continuously on, no reactions were observed until one reached about 120 cps,

whereupon the individuals in the swarms nearer than about 1.5 meters showed increased circling activity. As the dial went above this, the agitation increased and the swarms formed in front of the speaker. As the frequency became higher than 125 cps, the agitation diminished until, above about 130 cps, the swarm was again unaffected and resumed its ordinary position and level of activity. The same thing happened, but to a much greater degree, between about 230 and 270 cps, with the most agitated activity and attraction to the speaker at 250 cps.

An attempt was made, using 250 cps, to see whether swarms at horizontal distances beyond 1 to 1.5 meters could be attracted, but the maximum distance from which attraction could be induced was 1.5 meters. Beyond that, agitation and circling movements were induced, but the swarms did not approach the loud speaker. The best reactions were obtained with the swarms directly over the loud speaker or slightly above and within a horizontal distance of less than 1 meter from it. An attempt was made to move swarms which had been attracted to the speaker while the sound was on, but they would not follow the speaker. The swarms moved only for a short distance, then resumed their original positions. Apparently whatever stimulus afforded the swarm marker in this case was strong enough to draw the flies back.

Before more exact tests of the frequencies and intensities needed to induce these reactions were made, it was desirable to know how long one had to allow for clearly detectable reactions. For either the startle reaction or the agitated circling flight at a distance, the time was too short to be measured. The time needed for an agitated swarm to collect around a speaker was appreciable, however, and was determined 10 times each for 125 cps and 250 cps. The means and standard errors were: for 125, 7.0 ± 1.5 sec. (range = 2 to 16 sec.), and for 250, 4.5 ± 0.7 sec. (range = 2 to 8 sec.). It was thus necessary to allow about 10 sec. at each frequency for attraction, but the startle or agitated flight reaction could be determined almost instantaneously.

The time needed for the swarms to resume their original positions after attraction by a sound while the sound remained on continuously was 87 ± 12 sec. (range = 45 to 195 sec.), in 10 determinations. This allowed plenty of time for observation of this behavior pattern. To test whether the loss in reactivity was due to fatigue or adaptation, the insects were attracted by the 250 cps note and that was left on until they had stopped circling the speaker, whereupon the frequency was shifted to 125 cps, or the frequencies were used in reverse order. As soon as the new frequency was turned on, the swarms were reactivated and attracted. Thus, this would seem to be adaptation rather than fatigue.

Studies on Frequencies Inducing the Reactions.—With these preliminary observations in hand, a study was made using various frequencies of sound, to discover what frequencies were most effective. The first tests involved the startle reaction in many swarms at about 2 to 3 meters from the loud speaker. The same audio-oscillator was used to produce the essentially pure tones, with three speakers: the Jensen speaker described above for frequencies of 80 to 3,500 cps, a large "woofer" (Electro-Voice, Model 15 WK) for 30 to 300 cps, and a microphone used as a loud speaker (Altec, Model 633A) for 3,500 to 40,000 cps. The speakers were mounted on a tripod and this was placed at about 2 to 3 meters, horizontally, from a swarm, the selected frequency was set and the sound was turned on suddenly at full intensity. The results are summarized in the two columns on the left in table 1.

The reactions were obtained from 80 cps to 800 cps, with peak responses, actually complicated responses consisting of both the typical startle and the agitated circling, at 125 and 250 cps. The reaction units used in the table are arbitrary and subjective, but represent the judgment of four persons and involve only four levels of decision—barely perceptible reaction (+), definite but weak startle (++), strong, intense movements of all individuals (+++), and very intense reactions, almost dispersal (++++). Similarly extensive series of tests at frequencies from 1,000 to 40,000 cps gave entirely negative results. Many intermediate frequencies other than those listed in the table, were tried, and they gave results fully consistent with those presented.

The typical startle reaction, occurring at frequencies from 80 to 800 cps, was thus similar to that reported for *Cercyonis pegala* and *Ctenucha virginica* (Frings and Frings 1956, 1957) in being induced by a relatively wide band of frequencies. The agitated circling seemed to be a separate reaction, rather sharply tuned as to frequency.

To study the attraction, the speakers were set at horizontal distances of less than 1 meter from swarms, which were usually about 0.5 meters above the level of the speakers. The dials were set to give full output at the lowest or highest frequency, the sound was turned on and left on while the dial was turned very slowly through the frequency range. The results of numerous tests with many swarms are summarized in the two columns on the right in table 1.

Agitated circling and attraction of swarms was found only at 120 to 130 and 220 to 270 cps, with rather sharp peaks at 125 and 250 cps, the latter by far the stronger. Since 125 and 250 are harmonics, the region around 500 cps was carefully explored, but only rarely were reactions obtained, and these were very weak and probably represented startle reactions. Other harmonics and subharmonics of 250 and 125 cps were also given special tests, but no other frequencies were

found which induced the typical agitated attraction.

Here, then, was a rather nicely tuned receptor, and one was induced to ask whether this had any relationship to the wing sounds of males or females. Recordings were made of the wing sounds of the swarming males by holding a microphone (Electro-Voice, Model 655) in the swarm and recording with a tape-recorder (Ampex 350 P) at a tape speed of 15 in./sec. This was a difficult task, for the sound intensity produced by these small flies was very low, but, when ambient noise levels were low, it could be done. When these recordings were amplified and matched aurally by four persons with tones produced by an audio-oscillator, the frequencies were found to be 570 to 600 cps. As would be expected, playing these recorded wing sounds back to swarms induced no responses except a startle if the sound was turned on and off suddenly.

Unfortunately, no females were caught, so the frequency of the wing sound of the females could not be determined. The frequencies of female wing sounds of small Diptera are usually lower than those of the males (Sotavalta 1947; Roth 1948). Sotavalta (1947) has determined the wing sound frequencies of a few tendipedids, and the females of four of these have frequencies of 200 to 300 cps, while the males have frequencies of 400 to 500 cps. It is quite possible, therefore, that the frequency of the female wing sound in this species might be near 250 cps, but we do not know.

Because of the importance of a knowledge of the frequency of the female wing sound, much time was put in trying to secure females for recordings. Sweeping with insect nets yielded none. White or light green cloths were laid on the ground beneath or to the windward of the swarms in the hope that mated pairs might fall from the swarms and could thus be seen and captured. As soon as the cloths appeared beneath, however, the swarms moved 1 to 2 m. away. This definitely suggested that some visual swarm marker was involved, but none was obvious. If the cloths were put down before swarming time, however, the swarms formed at the usual places, but with reduced numbers. It was hoped, however, that some females might be captured, but none were, in spite of repeated attempts.

Studies on Intensities Inducing the Reactions.—We have shown previously (Frings and Frings 1956, 1957) that high intensity sounds, which probably have little biological significance, can induce startle reactions in insects. Up to this point in these tests, the intensities had been fairly high—80 to 85 db at 1 meter from the speakers. It seemed worthwhile to determine the minimal sound pressures (thresholds) needed to induce the responses. For this, sound pressures needed to induce agitated circling in swarms at a distance of about 2 meters were measured, rather than those needed for attraction. Later tests, however, showed that these thresholds were equally valid for the attraction as well.

Table 2.—Sound pressure thresholds for responses of swarms of *Pentaneura aspera*. The swarms were approximately 2 meters from the loud speaker.

Test no.	Ambient noise level (db)	Thresholds (db)	
		125 cps	250 cps
1	46–49	62	52
2	42–45	57	48
3	46–48	62	52
4	42–50	62	52
5	42–48	63	53
6	46–49	65	51
7	43–45	61	48
8	42–46	60	47
9	40–43	59	48
10	41–44	61	49
11	42–45	57	48
12	40–43	54	45
13	40–44	59	47
14	40–44	57	45
15	40–43	57	46
Ranges	40–50	54–65	45–53

Mean difference between thresholds for 125 cps and 250 cps..... 11.2±0.4 db (Range = 9–14)

Mean differences between thresholds and median ambient noise levels:

At 125 cps..... 15.9±0.4 db (Range = 13–18)

At 250 cps..... 4.8±0.4 db (Range = 3– 8)

The audio-oscillator was set for either 250 or 125 cps, the attenuator dial was set at an intensity high enough to induce the reaction, and the insects were stimulated. After they responded, the attenuator dial was turned down and the group retested. By allowing about 10 sec. between tests and making regular checks with effective intensities, adaptation or fatigue was ruled out. The intensity was first reduced in large steps until two adjacent settings were discovered at the higher of which a reaction was obtained and at the lower no reaction. The difference between those two critical settings was then reduced as far as practical. The procedure was repeated, starting with sound pressures below the threshold and increasing the intensities. While the operator of the sound equipment could usually see the reactions at this distance quite well, there were usually two other observers stationed near the swarms to check the movements. When the threshold was thus found, the sound pressure at the swarm was measured with a calibrated sound level meter (Scott, Type 410B).

At the same time, the ambient sound level was determined. These data are presented in table 2.

It is obvious that the sound pressures needed to induce the reactions were low—3 to 8 db. above ambient sound levels for 250 cps, and 13 to 18 db. for 125 cps. This must not be interpreted to mean that sound pressure levels of these magnitudes would be sufficient under silent conditions. Obviously only the effective frequencies in the ambient sound interfered with and should have been subtracted from the readings to get the actual thresholds, and these were unknown. But the levels were certainly much lower than those inducing startle reactions in other species. As a matter of fact, when intensities of sound at the swarms were above 80 to 85 db., dispersal of the swarms occurred. The startle reaction at frequencies other than the region about 125 and 250 cps, where the agitated circling masked it, was induced only with considerably higher sound pressures—20 to 30 db. above ambient sound levels.

The distances and thresholds at which the reactions could be obtained with sounds of 250 cps were also studied, and the data are presented in table 3. The thresholds were measured at 3 to 5 swarm positions for each distance and varied only by 2 to 3 db. from each other. It is interesting to note that, up to about 6 meters, the threshold intensity at the swarm is about the same as at shorter distances, but at distances over about 6 meters, the threshold intensities are higher. Why this should be so is not obvious.

Attempts to Locate the Receptors Involved.—The tendipedids are remarkable for the very bushy antennae of the males and the well developed Johnston's organs at the bases of the antennae. Since these are known to be sound receptors in mosquitoes, they might be assumed to be the receptors in this species. Unfortunately, no critical tests could be made. The small size of the insects made observations on the behavior in swarms of males from which antennae were removed impossible. An unsuccessful attempt was made to set up standing wave systems, to see whether the receptors were sensitive to velocity or pressure changes (Autrum 1936a, 1936b; Frings et al. 1948), by directing the sound toward a large board held at critical distances from the speaker. The setup, however, could be used only with swarms which were close to the speaker, and those moved away when such a device was installed nearby. Males were captured and housed in small cages to test for possible reactions in captivity, thus allowing observations under magnification. No reactions were found in caged males to any frequencies of sound. Unlike *Culicoides* spp. (Downes 1950, 1955), in which the antennal hairs of males are erected only when swarming, the hairs of these males were apparently always erected.

DISCUSSION

These results show that swarming males of this species give clear-cut reactions to sounds, and that the nature of the sounds needed to induce the reaction can be studied with precision. The results are disappointing, from a biological standpoint, because they give no indication of the significance of the reactions to sounds in the lives of the insects. The startle reaction, induced by relatively high intensities of sounds of many frequencies may be considered to be protective, causing the individuals to dart ahead when suddenly stimulated, thus making capture more difficult. The circling and attraction, however, which are much more precise and are evoked by specific frequencies, remain unexplained. Since the sound pressures needed to induce these reactions and the frequencies which are effective are well within the ranges normally encountered by individuals of this species in nature, one is inclined to believe that the reactions are related to normal behavior in some way. Certainly the fact that the receptor organs are so sharply tuned to special frequencies suggests an important role in the lives of these insects. We have, however, no hypotheses to offer at present which would be based on anything but sheer speculation. Furthermore, while such clear-cut indicator reactions would seem to be useful to study the organs involved in sound reception in this species, no way was found to do this.

Table 3.—Sound pressure thresholds for reactions to sounds at 250 cps by swarms of *Pentaneura aspera* at different distances between the swarms and the loud speaker.

Distance (m.)	Threshold (db)	Ambient noise (db)
2	50	45–47
4	51	44–47
5	49	44–46
6	48	42–44
7	58	44–47
8	60	46–50
10	62	44–46

One of the key deficiencies in this work is the lack of observations on females for determination of the nature of their wing sounds and for study of their behavior toward swarms. It is hoped that, through continued collection of swarms of this species, females may be found and studies of the wing tone and behavior of these can be made. In the meantime, the publication of the results so far may encourage others to make similar tests with swarming Diptera. Possibly with other species one may be able to use the reactions to sounds to elucidate the factors involved in swarming and mating in these flies.

REFERENCES CITED

Autrum, H. 1936. Über Lautäusserungen und Schallwahrnehmung bei Arthropoden. I. Untersuchungen an Ameisen. Eine allgemeine Theorie der Schallwahrnehmung bei Arthropoden. Zeitschr. vergl. Physiol. 23: 332–73.

1936. Eine Theorie der Schallwahrnehmung für Luftarthropoden. Verhandl. Deutsch. zool. Ges. 38: 125–34.

Child, C. M. 1894a. Beiträge zur Kenntnis der antennalen Sinnesorgane der Insecten. Zool. Anz. 17: 35–8.

1894b. Ein bisher wenig beachtetes antennales Sinnesorgan der Insekten, mit besonderer Berücksichtigung der Culiciden und Chironomiden. Zeitschr. wiss. Zool. 58: 475–528.

Davies, D. M., and **B. V. Peterson.** 1956. Observations on the mating, feeding, ovarian development, and oviposition of adult black flies (Simuliidae, Diptera). Canadian Jour. Zool. 34: 615–55.

Downes, J. A. 1950. Habits and life-cycle of *Culicoides nubeculosus* Mg. Nature 166: 510.

1955. Observations on the swarming flight and mating of *Culicoides* (Diptera: Ceratopogonidae). Trans. Roy. Ent. Soc. London 106: 213–36.

Frings, H., C. H. Allen, and **I. Rudnick.** 1948. The physical effects of high intensity air-borne ultrasonic waves on animals. Jour. Cell. and Comp. Physiol. 31: 339–58.

Frings, H., and **M. Frings.** 1956. Reactions to sounds by the wood nymph butterfly, *Cercyonis pegala*. Ann. Ent. Soc. America 49: 611–7.

1957. Duplex nature of reception of simple sounds in the scape moth, *Ctenucha virginica*. Science 126: 24.

1958. Uses of sounds by insects. Ann. Rev. Ent. 3: 87–106.

Gibson, N. H. E. 1945. On the mating swarms of certain Chironomidae (Diptera). Trans. Roy. Ent. Soc. London 95: 263–94.

Johnston, C. 1855. Auditory apparatus of the *Culex* mosquito. Quart. Jour. Microsc. Sci. 3: 97–102.

Kahn, M. C. 1947. Female mosquito "calls" and their possible significance in control. Kuba 3: 119–20.

Kahn, M. C., and **W. Offenhauser, Jr.** 1949. The first field tests of recorded mosquito sounds used for mosquito destruction. Amer. Jour. Trop. Med. 29: 811–25.

Nielsen, E. T., and **H. Greve.** 1950. Studies on the swarming habits of mosquitoes and other Nematocera. Bull. Ent. Res. 41: 227–58.

Nielsen, E. T., and **A. T. Nielsen.** 1953. Field observations on the habits of *Aedes taeniorhynchus*. Ecoolgy 34: 141–56.

Nielsen, E. T., and **H. T. Nielsen.** 1958. Observations on mosquitoes in Iraq. Ent. Meddel. 28: 282–321.

Offenhauser, W. H., Jr., and **M. C. Kahn.** 1949. The sounds of disease-carrying mosquitoes. Jour. Acoust. Soc. America 21: 259–63.

Reibisch, L. 1926. Über ein Gehörorgan bei Insekten. Schrift. naturwiss. Ver. Kiel 17: 177–80.

Risler, H. 1953. Das Gehörorgan der Männchen von *Anopheles stephensi* Liston (Culicidae). Zool. Jharb. (Abt. Anat. Ontog. Tiere) 73: 165–86.

Roth, L. M. 1948. A study of mosquito behavior. An experimental laboratory study of the sexual behavior of *Aedes aegypti* (Linnaeus). Amer. Midland Nat. 40: 265–352.

Roth, L. M., and **E. R. Willis.** 1952. Method for isolating males and females in laboratory colonies of *Aedes aegypti*. Jour. Econ. Ent. 45: 344.

Sotavalta, O. 1947. The flight-tone (wing-stroke frequency) of insects. Acta Ent. Fenn. 4: 1–117.

Tischner, H. 1953. Über den Gehörsinn von Stechmücken. Acustica 3: 335–43.

1954. Das Hören der Stechmücken. Attempto 4: 23–26.

1955. Gehörsinn und Fluggeräusch bei Stechmücken. Umschau 12: 368–70.

Tischner, H., and **A. Schief.** 1954. Fluggeräusch und Schallwahrnehmung bei *Aedes aegypti* L. (Culicidae). Verhandl. deutsch. zool. Ges. 1954: 453–60.

CHANGES IN BLOOD PROTEINS DURING THE DEVELOPMENT OF THE AMERICAN COCKROACH, PERIPLANETA AMERICANA[1]

A. L. STEINHAUER[2] AND W. P. STEPHEN
Department of Entomology, Oregon State College, Corvallis

ABSTRACT

Analyses by paper electrophoresis showed three protein fractions present in all stages of development except the egg, where only a single fraction was recovered. The fraction with the second greatest mobility was the most variable during the insect's development, always reaching a peak of concentration at and around times of molting, and disappearing between molts; it disappeared in adult males after 3 to 4 weeks and in adult females after 10 days. The first and third fractions showed variability that could be associated with development, but less strikingly. Fraction 3 also was present in greater proportion in adult females than in adult males.

Studies of insect blood proteins and their changes during the development of holometabolous insects have been reported by Drilhon (1954) and Stephen and Steinhauer (1957). Drilhon found the larvae of *Bombyx mori* (L.) to have two protein fractions, and that the more "distally migrating band" disappeared during the pupal stage. In the adult stage the distal band reappeared and the single proximal band was replaced by three weak fractions. Stephen and Steinhauer reported developmental changes in blood protein of two species of scarabs, *Lichnanthe rathvoni* (Lec.) and *Pleocoma oregonensis* Leach. In both species a marked qualitative change occurred.

[1]Aided by grants from the Graduate School Research Fund and the Basic Research Committee, Oregon State College. Technical Paper No. 1175, Oregon Agricultural Experiment Station. Accepted for publication March 25, 1959.

[2]Present Address: Dept. of Entomology, University of Maryland, College Park.

In *L. rathvoni* the apical positively migrating band disappeared between the larval and adult stages, and in *P. oregonensis* an additional negatively migrating band appeared in the adult stage.

Table 1.—Quantitative variation in the serum protein fractions through the development of fourth-stadium nymphs of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.38	0.21	0.41
2	.32	.23	.45
3	.28	.22	.50
4	.46	.17	.37
5	.43	.13	.44
6	.27	.14	.59
7	.36	.10	.54
8	.47	.00	.53
9	.31	.00	.69
10	.44	.00	.56
11	.28	.08	.64
12	.27	.14	.59
13	.34	.14	.52
14	.38	.15	.47
15	.35	.19	.46
16	.34	.22	.44
17	.29	.34	.37
18	.27	.39	.34

Table 2.—Quantitative variation in the serum protein fractions through the development of fifth-stadium nymphs of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.27	0.39	0.34
2	.39	.26	.35
3	.39	.17	.44
4	.33	.20	.47
5	.38	.12	.50
6	.33	.12	.55
7	.36	.08	.56
8	.25	.16	.59
9	.33	.08	.59
10	.33	.08	.59
11	.29	.08	.63
12	.27	.07	.66
13	.40	.00	.60
14	.41	.00	.59
15	.37	.00	.63
16	.34	.00	.66
17	.27	.13	.60
18	.31	.10	.59
19	.36	.08	.56
20	.32	.10	.58
21	.36	.13	.51
22	.29	.14	.57
23	.29	.15	.56
24	.35	.26	.49
25	.25	.44	.31

No comparable developmental studies have been conducted with hemimetabolous forms, although the protein fractions in various species of hemimetabolous insects have been reported. Clark and Ball (1956), Stephen and Steinhauer (1957) and Stephen (1958) have reported the protein fractions in the hemolymph of the American cockroach, *Periplaneta americana* (L.). Clark and Ball report six protein bands separable with paper electrophoresis from blood of specimens of all instars of the American cockroach.

MATERIALS AND METHODS

To determine developmental serum protein changes it was necessary to sample a single specimen repeatedly through its life cycle. The mortality resulting from the sampling of the early instars made it necessary to limit the selection of individuals for study to those beyond the third nymphal instar. However, pooled samples were run from individuals of the first three instars to determine the protein fractions present. Individuals from the fourth instar to the adult stage were large enough to allow several samplings at intervals of 1 to 2 weeks.

Single roaches in the late stages of development were isolated in petri dishes. These were sampled and their serum analyzed for proteins. Individ-

EXPLANATION OF PLATE

FIG. 1.—Paper strip with dyed protein fractions lying below Analytrol scan, showing pen-drawn curve, automatic integration, and relative concentration of each fraction.

FIG. 2.—Analytrol scan of veronal buffer extract of cockroach egg, showing application point and single fraction.

FIG. 3.—Analytrol scans of early, mid, and late fourth nymphal instars of the American cockroach.

FIG. 4.—Analytrol scans of early, mid, and late last nymphal instars of males of the American cockroach.

FIG. 5.—Analytrol scans of newly molted, 3-week-old, and 6-week-old adult males of the American cockroach.

FIG. 6.—Analytrol scans of early, mid, and late last nymphal instars of females of the American cockroach.

FIG. 7.—Analytrol scans of newly molted, 7-day-old, and 6-week-old adult females of the American cockroach.

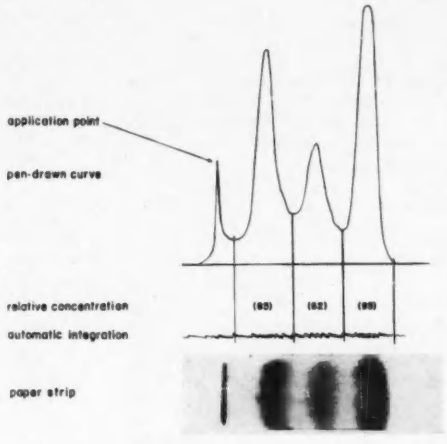


FIG. 1

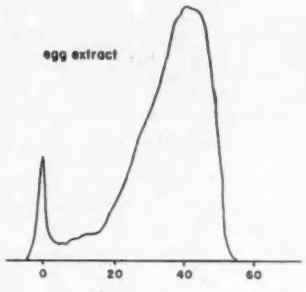


FIG. 2

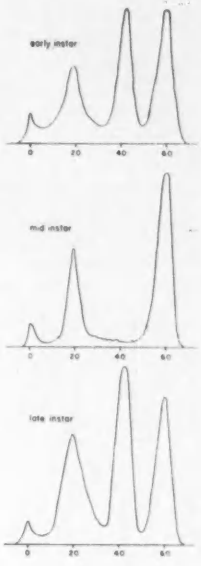
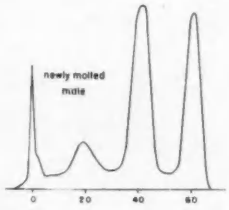
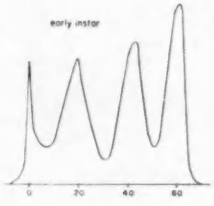
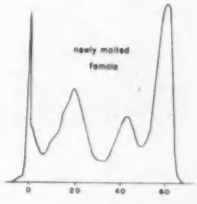
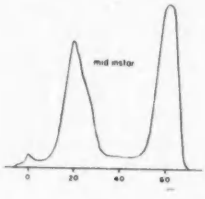


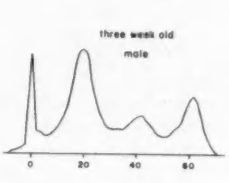
FIG. 3

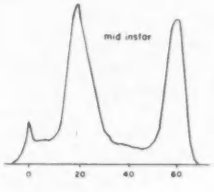


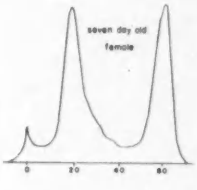


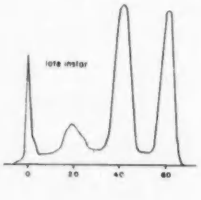


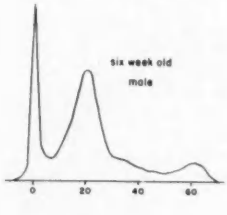


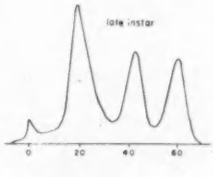












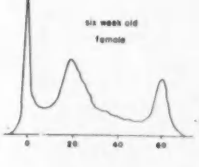


FIG. 4 FIG. 5 FIG. 6 FIG. 7

uals which had just molted were also sampled and isolated. The isolation permitted serum analysis of the same individual through a complete stage of development. Thus the experimenter was able to determine the changes occurring in the serum proteins through the development of the insect from the fourth instar to the adult stage.

Table 3.—Quantitative variation in the serum protein fractions through the development of last-stadium male nymphs of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.23	0.36	0.41
2	.36	.23	.41
3	.35	.25	.40
4	.33	.17	.50
5	.27	.23	.50
6	.32	.17	.51
7	.39	.04	.57
8	.38	.07	.55
9	.43	.06	.51
10	.35	.09	.56
11	.34	.06	.60
12	.30	.06	.64
13	.37	.11	.52
14	.36	.06	.58
15	.42	.00	.58
16	.29	.06	.65
17	.35	.05	.60
18	.32	.15	.53
19	.10	.21	.69
20	.09	.42	.49
21	.18	.48	.34

Table 4.—Quantitative variation in the serum protein fractions through the development of adult males of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.09	0.52	0.39
2	.22	.48	.30
3	.20	.44	.36
4	.33	.37	.30
5	.26	.41	.33
6	.55	.18	.27
7	.58	.20	.22
8	.73	.15	.12
9	.55	.17	.28
10	.70	.09	.21
11	.74	.00	.26
12	.78	.00	.22
13	.75	.00	.25
14	.74	.00	.26
15	.72	.00	.28
16	.78	.00	.22
17	.80	.00	.20
18	.87	.00	.13
19	.84	.00	.16
20	.88	.00	.12
21	.88	.00	.12
22	.87	.00	.13

Although the data resulting from pooled samples of the early instars did not have the objectivity of the individual analyses made on the later stages, they served as an indication of the qualitative and quantitative protein composition of serum at these early stages. Pooled samples of egg extract from single egg cases were also analyzed for protein fractions.

Extraction of blood samples was accomplished by direct heart puncture through the dorsal intersegmental membrane. The blood was drawn into a 10-microliter micropipette and transferred to a sample applicator. The blood was then immediately applied to a filter paper strip for electrophoretic analysis.

The analyses for protein fractions were conducted on a Spinco Model R paper electrophoresis system (Beckman, Spinco Division) with a Durrum-type vertical cell. A veronal buffer, with a pH of 8.6 and ionic strength of 0.05, prepared after Block et al. (1955), was used.

The electrophoresis was conducted at a current of 2.5 ma per cell for a period of 16 hours. At the completion of a run, the strips were heated in an oven at 110°–120° C. for 30 minutes prerinsed, in purified methanol (CP) for 15 minutes, and stained in bromphenol blue (Spinco Dye B–4) for 30 minutes. Staining was followed by three consecutive 6-minute rinses in 5 percent aqueous glacial acetic acid. The strips were then blotted and dried for 15 minutes at 110°–120° C.

The strips were scanned on the Spinco R Analytrol. Just prior to scanning, the strips were exposed to ammonia vapors for 15 minutes to bring out the maximum dye intensity. The Analytrol scans provided a graphic presentation of the protein fractions and an estimate of the area under the curve (fig. 1). The relative concentrations of the various protein fractions were determined and then transposed to values representing percent of total protein per sample.

RESULTS

Serum protein analysis of American cockroach blood with paper electrophoresis yielded two or three distinctly separable fractions. The first fraction migrated 19 mm., the second 43 mm., and the third 61 mm. from the point of application under the conditions of this experiment. There was also a distinct band at the application point, but it is felt (Stephen 1958) that this is primarily oxidized melanin and coagulum, and it was not, therefore, included as a distinct protein fraction in the computation of results. All of the other three fractions were found in all stages except the egg. The second fraction exhibited the greatest

degree of quantitative variability and was not recoverable during certain periods of each stage of development.

Paper electrophoresis of veronal buffer extracts of American cockroach eggs yielded only one broad fraction with motility of approximately 39 mm. from the point of application (fig. 2).

All three fractions were recovered from the pooled samples of each of the first three instars. The first fraction of the first instar was very weak in comparison to the first fraction of the later instars. The second and third fractions were present in concentrations comparable to those of later instars. Direct comparisons with the later instars cannot be made since the use of pooled samples negates individual variation and renders the interpretation of developmental variation impossible.

Tables 1 and 2 illustrate the quantitative variation in the serum protein fractions in the fourth and fifth instars, respectively. The same pattern of change is exhibited in both stadia. The samples are arranged chronologically in each table to show the protein composition of the serum at the beginning of the stadium, followed by samples extracted from individuals at the various intermediary stages of development, and ending with individuals sampled just prior to molting. In both instars the second fraction shows the greatest amount of change. It is present in a high relative concentration at the beginning and end of the stadium but is completely absent at a point midway between the two molts. Fraction 1 is present in approximately the same concentration throughout the stadium while fraction 3 shows an increase around the midpoint of the stadium. Figure 3 is a reproduction of the densitometer scans at the beginning, middle, and end of the fourth stadium, which closely resemble the same three stages of development for the fifth stadium.

The serum protein fractions of the last stadium male nymphs exhibit a change similar to those of fourth and fifth stadia with the exception that fraction one decreases in relation to the other two fractions at the end of the stage (table 3, figure 4).

In the male adult the first fraction shows a steady increase in relation to the other bands. Fraction two decreases until it finally disappears 3 to 4 weeks after the adult molt, and fraction 3 decreases until about the fourth week of the adult stage, at which time it and fraction 1 reach a stable quantitative relationship (table 4, figure 5).

During the last stadium of female nymphs the changes in serum protein composition are again similar to those of the fourth and fifth instars. Fraction 1 remains at a relatively constant concentration. Fraction 2 shows a decrease from the beginning to the middle of the stadium, with a corresponding increase toward the end of the stadium. Fraction 3 increases from the beginning to the middle of the stadium, with a decrease just prior to molting to the adult stage (table 5, figure 6). After the adult molt, the second

Table 5.—Quantitative variation in the serum protein fractions through the development of last-stadium female nymphs of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.25	0.44	0.31
2	.30	.34	.36
3	.29	.23	.48
4	.28	.21	.51
5	.36	.21	.43
6	.35	.12	.53
7	.38	.13	.49
8	.42	.05	.53
9	.31	.11	.58
10	.44	.07	.49
11	.35	.07	.58
12	.33	.05	.62
13	.40	.04	.56
14	.36	.04	.60
15	.53	.00	.47
16	.38	.08	.54
17	.37	.05	.58
18	.37	.00	.63
19	.35	.07	.58
20	.44	.06	.50
21	.36	.07	.57
22	.35	.16	.49
23	.38	.24	.38

Table 6.—Quantitative variation in the serum protein fractions through the development of adult females of the American cockroach, expressed as fractions of the total protein.

Individual No.	Protein fraction		
	No. 1	No. 2	No. 3
1	0.52	0.24	0.24
2	.38	.16	.46
3	.54	.00	.46
4	.72	.00	.28
5	.78	.00	.22
6	.76	.00	.24
7	.55	.00	.45
8	.59	.00	.41
9	.63	.00	.37
10	.55	.00	.45
11	.63	.00	.37
12	.82	.00	.18
13	.75	.00	.25
14	.57	.00	.43
15	.74	.00	.26
16	.58	.00	.42
17	.40	.00	.60
18	.60	.00	.40
19	.77	.00	.23
20	.70	.00	.30
21	.75	.00	.25

fraction decreases rapidly, disappearing within 10 days. Fraction 1 remains at approximately the same concentration throughout the stage, although it shows an increase in relation to fraction 3 which decreases somewhat in concentration during the first 2 weeks of the adult stage (table 6, figure 7).

DISCUSSION

The appearance of three protein fractions in the serum of the American cockroach disagrees with both previously published accounts of the blood protein composition of this insect. Clark and Ball (1956), using a different analytical procedure, reported six fractions in American cockroach blood. During the present work over 300 individuals were analyzed, and in no case were more than three fractions separable in the quantities of blood analyzed. Fraction 1 in these studies is noticeably broader than either of the other two. This suggests that it may be made up of several proteins, all having approximately the same mobility in the buffer system used for this study.

The occurence of only two fractions in American cockroach blood was reported previously by the authors (Stephen and Steinhauer 1957, Stephen 1958). The two fractions recorded were comparable to fractions 1 and 3 of the present work. The reason for this discrepancy is that only male and female adults were analyzed for serum protein composition, and the individuals used were of an age where fraction 2 had already disappeared.

An interesting observation is the close association of fraction 2 with the molting cycle of individuals. Every individual sampled either shortly before, during, or shortly after molting, showed a high relative concentration of fraction 2. This fraction always disappeared between molts. The physiological implications of this phenomenon are unknown. It appears certain that the metabolic changes occurring at molting are either the cause of, or the effect of, these changes in the serum protein. Further work is necessary before any definite significance can be attached to these observations, but speculation as to the implications of these blood protein changes is warranted.

Minor fluctuations in the third fraction appeared to be associated with molting, although quantitative changes were not as marked as those of the second fraction. The third fraction increases to a peak between molts and decreases prior to molting. A sexual difference observed in this fraction confirms a similar observation by Stephen and Steinhauer (1957). Although fluctuating more widely in female adults than in male adults, the third fraction was proportionately greater in the females and never approached the low levels common in the mature males.

The proportion of fraction 1 remained at a relatively constant level throughout the nymphal development, but dropped considerably at the end of the last stadium of males. It increased again during the adult stage and finally represented over 80 percent of the total serum protein.

REFERENCES CITED

Block, R. J., E. L. Durrum, and **G. Zweig.** 1955. A manual of paper chromatography and paper electrophoresis. New York: Academic Press. 484 pp.

Clark, E. W., and **Gordon H. Ball.** 1956. Preliminary microelectrophoretic studies of insect proteins. Physiol. Zool. 29: 206–12.

Drilhon, A. 1954. Étude électrophorétique des protéines de l'hémolymphe du *Bombyx mori* au cours du son cycle de croissance. Compt. rend. Acad. Sci. 238: 2452–4.

Stephen, W. P. 1958. Hemolymph proteins and their use in systematic studies. Proc. 10th Internatl. Congr. Ent. (1956) 1: 395–400.

Stephen, W. P., and **A. L. Steinhauer.** 1957. Sexual and developmental differences in insect blood proteins. Physiol. Zool. 30: 114–20.

TRAVEL GRANTS

The National Science Foundation has made funds available to the Entomological Society of America for the purpose of partially defraying travel expenses of a limited number of U. S. scientists to the XIth International Congress of Entomology in Vienna, Austria, August 17-25, 1960. The grants will approximately cover round-trip air-tourist fare from the applicant's home to Vienna.

Application blanks may be obtained by writing to R. H. NELSON, Executive Secretary, ENTOMOLOGICAL SOCIETY OF AMERICA, 1530 P Street N.W., Washington 5, D.C. Closing dates for applications will be January 15, 1960, and the awards will be announced in February.

HOST RANGE STUDIES OF THE MELON LEAF MINER, LIRIOMYZA PICTELLA (THOMSON) (DIPTERA: AGROMYZIDAE)[1]

EARL R. OATMAN[2]

ABSTRACT

A full life cycle was completed on 54 out of the 71 species and varieties of wild and cultivated plants that were tested. These "positive" species, representing 16 of the 21 plant families sampled, were listed as severely, moderately, or lightly mined, according to the numbers of larvae completing their development in the leaves. Most of the heavily mined species were in the Leguminosae, Compositae, and Cucurbitaceae. Several plant families included both positive and negative host species; and several species (e. g., common egg plant and snapdragon) exhibited hypersensitive reactions to the presence of the mining larvae.

The melon leaf miner, *Liriomyza pictella* (Thomson) mines the leaves of both cultivated and uncultivated plants. Cultivated hosts include alfalfa, aster, beans, cantaloupes, Cranshaw melon, cotton, dahlia, and zinnia. The weed hosts include *Datura meteloides* D.C., *Helianthus annuus* L., *Malva borealis* Wallm., *Medicago lupulina* L., *Stachys californica* Benth., and *Vicia gigantea* Hook. (Frick 1957).

During field research in the Patterson area of the San Joaquin Valley, California, this insect pest caused economic damage to all varieties of melon, and several varieties of beans and alfalfa (Oatman and Michelbacher 1958). The presence of similar mines in the leaves of tomato and other cultivated plants, ornamentals, and weeds in nearby fields, gardens, and waste places posed the question as to whether or not these mines could have been produced by the melon leaf miner. Therefore, studies were undertaken in 1955 to determine the host range of the melon leaf miner.

METHODS AND MATERIALS

The tests were conducted under greenhouse conditions. Each test plant was placed in the center of a large culture cage containing high populations of adult melon leaf miners on Henderson's bush lima bean plants (Oatman and Michelbacher 1958). Generally there were 20 to 30 bean plants in each culture cage.

The test plant was left inside the cage for 3 days, then removed and placed on a cloth-covered surface for observation. The plant was examined for the presence of egg and feeding punctures, and for mines. Larvae that emerged to pupate were collected and placed in ventilated vials, and were observed later for the emergence of adults. If mines did not develop on the plant within 3 to 5 days, the process was repeated. If mines were not obtained from the second test, it was repeated again. If, after this, the results were still negative, the plant was classified as a negative host plant. In those experiments where the adults fed and oviposited, and larvae, pupae, and adults were obtained, the plant was considered a positive host plant. In several instances where pupae were not obtained, even though many eggs and mines were present, the plant was retested after it had grown more mature leaves. If the plant was an older one, and the miners did not complete their development, a new young plant was later tested whenever possible. The positive host plants were arbitrarily listed as being severely, moderately, or lightly mined. The life stage to which the insect developed was noted for each negative plant tested.

Many of the weeds tested were obtained from fields in the Patterson area and transplanted and cultured in the greenhouse. Others were taken from the area around the University greenhouses. The vegetable, flower, and field-crop plants were grown in the greenhouse from seeds, or were taken from stock plants already under cultivation.

RESULTS AND DISCUSSION

In all, 71 species and varieties of plants, representing 21 families, were tested. Of these, 54 species were classified as positive and 17 as negative, with 16 plant families represented in the positive group and 13 in the negative group. Both positive and negative species were found in eight families.

The positive host plants[3] were as follows.

LEGUMINOSAE

Medicago sativa L., alfalfa***
Phaseolus limensis Macf., lima bean, Fordhook variety***
Phaseolus limensis Macf., lima bean, Henderson's bush lima variety***
Pisum sativum L., garden pea***
Lupinus spp., lupine***
Melissa officinalis L., garden balm***
Trifolium pratense L., red clover***

[1]Portion of a dissertation submitted to the Graduate Division of the University of California, Berkeley, in partial satisfaction of the requirements for the degree Doctor of Philosophy. Accepted for publication March 28, 1959.

[2]Formerly graduate research assistant in the Department of Entomology and Parasitology, University of California, Berkeley. Presently Assistant Professor, Department of Entomology, University of Wisconsin, Madison.

[3]***=severely mined; **=moderately mined; *=lightly mined.

Melilotus alba Dear., white melilot**
Melilotus indica All., yellow melilot**
Trifolium repens L., white clover*
Trifolium hybridum L., alsike clover*
Trifolium fragiferum L., strawberry clover*

COMPOSITAE

Aster spp., aster***
Tagetes spp., marigold***
Sonchus oleraceus L., common sow thistle***
Senecio vulgaris L., common groundsel***
Silylium marianum Gaertn., milk thistle**
Chrysanthemum leucanthemum L., ox-eye daisy*
Helianthus annuus L., common sunflower*
Zinnia spp., zinnia***
Felicia bergeriana O. Hoffm., cineraria**

CUCURBITACEAE

Cucumis melo reticulatus L., cantaloupe***
Cucumis melo L., Cranshaw variety***
Cucumis melo L., casaba variety***
Cucumis melo L., honeydew variety***
Cucumis melo L., Persian variety***
Cucumis melo L., Santa Claus variety***
Citrullus vulgaris Schrod., watermelon***
Cucumis sativus L., cucumber**
Cucurbita maxima Duschene, squash*

SOLANACEAE

Solanum melongena esculentum Nees, common egg plant**
Datura meteloides D.C., Tolgaucha**
Physalis lanceifolia Nees., lance-leaved ground-cherry**
Lycopersicum esculentum Mill., common field tomato*
Capsicum frutescens grossum Bailey, bell pepper*
Solanum tuberosum L., common field potato*

CRUCIFERAE

Raphanus sativus L., wild radish*
Brassica campestris L., common yellow mustard*
Brassica spp., smooth leaf mustard*
Nasturtium spp., nasturtium*

MALVACEAE

Malva rotundifolia L., dwarf mallow**
Gossypium hirsutum L., upland cotton**

RANUNCULACEAE

Aquilegia spp., columbine*
Ranunculus spp., buttercup*

CHENOPODIACEAE

Spinacia oleracea L., spinach*
Chenopodium album L., lamb's quarter*

POLYGONACEAE

Polygonium aviculare L., wiregrass**

ROSACEAE

Prunus andersonii Gray, desert peach*

AMARANTHACEAE

Amaranthus retroflexus L., rough pigweed***

UMBELLIFERAE

Apium graveolens L., common celery***

GRAMINEAE

Hordeum vulgare, barley*

ACANTHACEAE

Plantago major L., broad-leaved plantain*

EUPHORBIACEAE

Ricinus communis L., castor bean*

SCROPHULARIACEAE

Antirrhinum majus L., snapdragon*

Numerous eggs and larvae were present in the leaves of common sunflower and broad-leaved plantain, but only a few adults were obtained. In the latter plant the larvae usually died after producing a mine about ½-inch long; adults were finally obtained in the third test. Large numbers of egg and feeding punctures were seen on the common egg plant, but few of the miners developed to the adult stage. Several larvae were observed in the leaves of lamb's quarter, but only one adult was obtained in the three tests conducted. Many eggs and larvae were present in the cotyledons of upland cotton plants, but the larvae always died. Larvae developed only in the older basal leaves of snapdragon; those in younger leaves were destroyed by welt-like wound tissue formation. A second type of hypersensitive plant reaction was that resulting from the presence of miners in the common egg plant; the tissue dried up around the area containing the larvae, thus terminating their development.

The negative plants were as follows.

AMARANTHACEAE

Amaranthus hybridus L., green amaranth
Amaranthus graecizans L., tumbleweed

CHENOPODIACEAE

Beta spp., sugar beet

CARYOPHYLLACEAE

Stellaria media (L.) Cyr., common chick weed

COMPOSITAE

Chrysanthemum spp., chrysanthemum

CRUCIFERAE

Matthiola spp., garden stock

JUGLANDACEAE

Juglans sp., English walnut

LILIACEAE

Lilium sp., lily

POLYGONACEAE

Rumex crispus L., curly dock
Polygonium lapanthifolium L., common knot weed

ROSACEAE

Fragaria spp., strawberry, Shasta variety
Fragaria spp., strawberry, Klondike variety

SOLANACEAE

Nicotiana spp., common tobacco
Solanum pseudo-capsicum L., Jerusalem cherry

SCROPHULARIACEAE

Mimulus guttatus D.C., common monkey flower

VITACEAE

Vitis vinifera L., wine grape

Although 17 of the 71 plants tested were classified as negative or nonhosts, almost 50 percent of the negative plants were utilized to some degree by the melon leaf miner. In two of the negative plants, common monkey flower and common chick weed, a few pupae were

obtained but the adults failed to emerge. This could have been natural mortality. Numerous eggs were deposited in garden stock; however, the larvae all died after mining for distances of ⅛ to ¼ inch. Fertile eggs were also deposited in tumbleweed, bindweed, tobacco, and Jerusalem cherry, but none of the mining larvae completed their development. Eggs and feeding punctures were observed on chrysanthemums, but the eggs failed to hatch. The remaining plants classified as nonhosts had neither egg punctures nor feeding punctures within the leaves.

The results of this host-range study show that the melon leaf miner has a wide distribution, occurring on a large number and wide variety of plants. This, together with the large number of species of hymenopterous parasites associated with it, indicates that *L. pictella* is indigenous to the San Joaquin Valley of California.

The wide range of plants which served as hosts for the melon leaf miner serve also as hosts, in the field, for other agromyzid species. These include several very important, closely related species of *Liriomyza*, among them the tomato leaf miner, *Liriomyza munda* Frick. These studies thus indicate the necessity for, and the desirability of rearing large series of adults from the mined plants under observation and sending them to a specialist for positive identification.

REFERENCES CITED

Frick, K. E. 1957. Nearctic species in the *Liriomyza pusilla* complex. No. 2. *L. munda* n. sp. and two other species attacking crops in California (Diptera: Agromyzidae). Pan-Pacific Ent. 33(2): 59–70.

Oatman, E. R., and **A. E. Michelbacher.** 1958. The melon leaf miner, *Liriomyza pictella* (Thomson) (Diptera: Agromyzidae). I. Life history studies. Ann. Ent. Soc. America 51(6): 557–66.

THE NATURAL ENEMIES OF THE HORNWORMS ON TOBACCO (LEPIDOPTERA: SPHINGIDAE)[1, 2]

FRANCIS R. LAWSON

Entomology Research Division, Agric. Res. Serv., U. S. D. A.

ABSTRACT

The known enemies of the hornworms *Protoparce sexta* (Johan.) and *P. quinquemaculata* (Haw.) are listed. In North Carolina the most important are the neidid hemipteron *Jalysus spinosus* (Say), which attacks eggs; the vespid wasps *Polistes fuscatus* (F.) and *P. exclamans* (Vier.), which are predators of larvae; and the braconid parasite *Apanteles congregatus* (Say). Two tachinid Diptera, *Zygosturmia protoparcis* (Towns.) and *Winthemia* sp., are seldom more than minor enemies. In 37 populations the average mortality of hornworms was nearly 98 percent. More than half of this was due to the wasps, which killed a high percentage of the parasites along with the hosts. The mortality varied with time and place, but the proportions caused by different enemies remained about the same.

The hornworms *Protoparce sexta* (Johan.) and *P. quinquemaculata* (Haw.) have been major pests of tobacco in the United States for many years. A general program of research on the biology and control of these pests has been conducted in North Carolina since 1952, in cooperation with North Carolina State College and Department of Agriculture. The research included an investigation of the natural enemies and their effect on hornworm populations. This phase will be reported here. Most of this work was done at Oxford.

In these studies the primary objective was to measure the effect on hornworm populations of those natural enemies that kill a significant fraction of the eggs and larvae. No attempt was made to identify all the minor enemies. Little effort was expended on enemies of pupae and none at all on those attacking adults. It is very difficult to find and observe these stages. Pupae are buried deep in the soil, and adults are scarce and well concealed during the day.

METHODS OF STUDY

Hornworm populations were determined by counting eggs and larvae on 25 to 50 marked plants in ½-acre plots of unsprayed tobacco at intervals of 1–2 days. A continuous record was kept on each hornworm found in an attempt to follow it through its larval life. It was identified by tagging the leaf on which it was seen and recording the species and size. Since the two species cannot be separated with certainty before the fourth instar, records of mortality prior to that stage have been combined.

Whenever possible the cause of death was determined. Larvae from which parasites had

[1]Accepted for publication April 6, 1959.

[2]R. L. Rabb, North Carolina State College, was responsible for the data taken at McCullers and Clayton, and W. B. Crews and M. B. Peace did much of the routine work.

Table 1.—Percentages of hornworms in the field identified as *Protoparce sexta*, Oxford, N. C.

Brood	1952		1953		1954	
	Number of larvae	Percent *sexta*	Number of larvae	Percent *sexta*	Number of larvae	Percent *sexta*
1	79	58	28	68	21	90
2	120	82	78	91	35	77
3	57	100	79	95	23	91

emerged were assumed to be killed by the parasites, although such larvae do not actually die for several days and in the meantime may be carried away by predators. Dead larvae that showed no external evidence of parasitism or predation were assumed to have died from disease. Many such larvae were moribund or showed other symptoms before or after death. Predation was difficult to determine. Occasionally a predator was seen attacking a larva. Frequently all or part of a hornworm showing marks of predation was found. More often, such larvae simply disappeared without a trace. These were listed as missing, but since precautions had been taken to prevent migration from one plant to another, most of the missing hornworms were probably killed by predators.

GENERAL BIOLOGY OF THE HORNWORMS

Metcalf (1909) stated that at least 90 percent of the hornworms found in the field in North Carolina were *P. sexta*. Table 1 gives recent data from Oxford on this point.

Metcalf reported that the hornworms attacked various solanaceous plants. Madden and Chamberlin (1945) indicated that the larvae were confined to this family but preferred tobacco, although tomatoes, eggplants, peppers, and various weeds were also attacked. The adults were observed to feed on several families of night-blooming flowers with tubular corollas, including tobacco. In the Oxford area and throughout most of the State, tobacco is so much more abundant than any other host of the larvae that it is, for practical purposes, the only host.

Alwood (1898) reported that eggs were nearly always laid on the under side of the leaf. Metcalf said that they were occasionally found on the upper surface. Gilmore (1938a) reported 74 percent on the lower surface, usually near the tip of the leaf. Madden and Chamberlin found 78 percent on the lower surface of the leaf. They also found that 57 percent of the eggs were laid on the upper third of the plant, 39 percent on the middle third, and only 4 percent on the lower third. Similar observattions have been made by a number of workers in North Carolina.

Metcalf reported two broods of hookworms and a partial third in North Carolina. He said that the first brood originated from overwintering pupae, the second partly from the same source and partly from the first brood. The source of the third brood was not given. This author said, "No definite number of generations of hornworms can be given for North Carolina." With minor exceptions the studies at Oxford support Metcalf's statements. When tobacco stalks were left in the field, the third brood was complete in 1953 and 1954, and nearly complete in 1952. However, in a large proportion of tobacco fields the stalks are destroyed before the third brood pupates. Both species of hornworms pupate in the soil. According to Gilmore (1938a), both species have five, rarely six, larval instars in Tennessee. Madden and Chamberlin confirmed this in Florida for *P. sexta*.

Table 2.—Parasitization by *Apanteles congregatus* of hornworms of different sizes when collected in the field and reared in the laboratory, Oxford, N. C.

Instar collected	Collected Aug. 31 to Sept. 24, 1953		Collected Sept. 16–30, 1954	
	Number	Percent parasitized	Number	Percent parasitized
Egg	24	0	—	—
1	44	43	20	25
2	30	77	55	40
3	18	78	36	44
4	24	96	31	71
5	5	80	7	29

EGG PARASITES

Ashmead (1887) bred *Trichogramma minutum* (*pretiosa*) Riley from eggs of *P. sexta* in Florida. The same parasite was mentioned by Garman (1897) from Kentucky, and was bred by Gilmore (1938a) from *P. sexta*. Ashmead described *Telenomus sphingis* (*monilicornis*) (Ashm.) from *P. sexta* in Florida, and the same species has been recorded from Brazil by Guimarães (1925), from Puerto Rico by Wolcott (1922), and from St. Vincent, Santo Domingo, and Tennessee by Gahan (1930). Gilmore (1938a) listed this species and *T. nigriscapus* Ashm. from Kentucky

and Tennessee. *T. connectans* Ashm. was recorded from St. Vincent and Santo Domingo by Gahan. Madden and Chamberlin report that F. L. McDonnough found some egg parasites tentatively identified as serphids (now family Prototrupidae) in Florida in 1917. No parasitized eggs have been found in North Carolina out of many hundreds examined.

Table 3.—Emergence of parasite *Apantales congregatus* and its hyperparasite from hibernation and light-trap catches of its sphingid hosts, Oxford, N. C.

Date 1953	Number of parasites emerging		Number sphingids caught	
	A. congregatus	*Hypoptero-malus tabacum*	*Protoparce* spp.	Other[a]
April 8	0	2	—	—
9	0	2	—	—
13	0	17	—	—
16	0	23	—	—
17	0	16	—	—
20	3	38	—	—
21	0	12	—	—
22	0	25	—	—
23	0	19	—	—
25	4	71	—	—
27	12	41	0	0
28	6	9	0	0
29	6	17	0	0
30	15	7	0	2
May 1	3	4	0	0
4	31	4	0	12
5	10	0	0	6
6	8	0	0	3
7	5	1	0	0
8	0	0	0	0
9	3	0	—	—
10	0	0	—	—
11	0	0	1	8
12	1	0	3	9
13	1	0	0	12
14	—	—	3	15
15	0	1	3	16
Total	108	309		

[a]Three specimens of *Atriedes plebeja* (F.) and one of *Darapsa pholus* (Cramer), all others *Celerio lineata* (F.).

PARASITES OF LARVAE

Apanteles congregatus (Say) has been recorded as common or abundant in Virginia (Alwood 1898), Oregon (Lovett 1915), Kentucky (Garman 1897), and Georgia (Reed 1915). Madden and Chamberlin (1945) obtained only three records of this parasite from thousands of hornworm larvae in Florida, but Quaintance (1898) considered it important. Kuitert and Tissot (1956) said that the parasite was occasional in Florida. Thompson (1946) listed this species from Canada. It also occurs in Brazil (de Azevedo 1924), Jamaica (Gowdey 1923), and Central America (Muesebeck et al. 1951). At least four other species in the same genus attack subspecies of *P. sexta* in Central and South America. Porter (1918, 1920) recorded *A. reedi* Porter from Argentina and *A. riverae* Porter from Chile. Gowdey (1925) listed *A. americanus* (Lep.) from Jamaica. Muesebeck et al. included Central and South America and the southern United States in the distribution of this species. Bruner and Scaramuzza (1936) recorded *A. flavicentris* (Cress.) in Cuba. Peluffo (1923) found *Apanteles* sp. in Uruguay.

Gilmore (1938b) discussed the biology of *A. congregatus* in Tennessee, and Fulton (1940) described the developmental stages and habits. Gilmore reported that oviposition occurred most frequently in the second and third instars of the host larvae and did not record parasitization in the first instar. According to Fulton, eggs and sometimes small larvae were found in many first-instar hornworms; most second instars contained both eggs and small larvae, but some only small larvae; third instars usually contained larvae, but a few eggs could be found.

Table 2 shows the results of rearing host larvae at Oxford in 1953 and 1954. Since these hornworms were collected in the field and reared individually in covered petri dishes, any parasites that emerged must have been deposited in them before capture. A large proportion were parasitized in the first instar. The parasites emerged from fourth and fifth instars but rarely from the third. About two-thirds of those deposited in first instars emerged from fourths and about one-third from fifths.

Gilmore (1938b) found that *P. sexta* was the preferred host in Tennessee. In North Carolina there seems to be little difference. Records for three years show that 35.8 percent of 81 *P. quinquemaculata* and 42 percent of 788 *P. sexta* larvae were parasitized.

According to Muesebeck (1921), *A. congregatus* has been reared from 12 species of sphingids, but from no other family. In North Carolina the hornworms on tobacco are by far its most abundant hosts, but it appears to be rather poorly synchronized with them. On October 21, 1952, 1,000 cocoons of this parasite were mixed with plant debris and placed on the surface of the soil in an earthenware pot out-of-doors at Oxford. In the spring a cloth funnel was arranged over the pot so that any parasites emerging would be trapped in a vial. Emergence records of *A. congregatus* and its most abundant hyperparasite, *Hypoptermalus tabacum* (Fitch), in comparison with light-trap catches of *Protoparce* and other sphingids, are given in table 3. The first sphingids were caught at about the peak of *Apanteles* emergence, but the first *Protoparce* were not caught until near the end of the emergence period. The first hornworm larvae appeared on tobacco May 22, 9 days after the last *Apanteles* had emerged and about 3 weeks after the peak of emergence.

Table 4.—Weight distribution of field-collected larvae of *Protoparce sexta* parasitized by tachinids compared with unparasitized and pupating larvae, Oxford, N. C.

Weight (Grams)	1952				1953			
	June 27 to July 10			Number pupating Aug. 10–15	June 22			Number pupating July 2–Sept. 28
	Tachinid eggs per larva	Number of larvae			Tachinid eggs per larva	Number of larvae		
		Parasitized	Not parasitized			Parasitized	Not parasitized	
1–1.9	0	0	2	0	0.2	1	4	0
2–2.9	0	0	3	0	2.2	3	1	0
3–3.9	0	0	9	1	4.8	3	2	0
4–4.9	0	0	5	4	23.4	12	1	2
5–5.9	2.8	2	4	2	19.8	12	0	3
6–6.9	2.7	7	7	2	28.1	7	1	7
7–7.9	5.7	9	3	5	16.3	3	0	3
8–8.9	4.7	5	4	3	—	0	0	1
Total	—	23	37	17	—	41	9	16
Percent	—	38.3	61.7	—	—	82.0	18.0	—

Garman (1897) reared *Mesochorus luteipes* Cress. and *H. tabacum* from hornworms along with *A. congregatus*, and believed them to be secondaries. Madden and Chamberlin recorded *H. tabacum* as a hyperparasite in Florida. Gilmore (1938b) listed this species, and also *Eupteromalus viridescens* (Walsh), *Horismenus floridanus* (Ashm.), and *Pediobius* sp. Fulton (1940) found *H. tabacum*, *H. floridanus*, *Isdromas mesochori* (Ashm.), *Spilochalcis side* (Walk.), and *Ceratosmicra* n. sp. as hyperparasites in North Carolina. *H. tabacum* was the most important hyperparasite of *A. congregatus* from tobacco fields, and the parasitization ranged from 19 to 100 percent in September 1937. At Oxford in 1952 a few lots of *A. congregatus* cocoons reared during the summer failed to show any hyperparasites, but the cocoons collected in October of that year (table 3) showed heavy parasitization the following spring. This hyperparasite emerged earlier than its host. There are two records of ectoparasites on P. sexta—*Euplectrus plathypenae* Howard (Gilmore 1938a), and the midge *Forcipomyia fuliginosa* (Meig.) (Wirth 1956).

TACHINID PARASITES OF LARVAE AND PUPAE

In contrast to the braconid parasites of the hornworms, which have one primary species common throughout the United States, the dipterous parasites comprise many species. Gilmore (1938a) found at least eight in the Tennessee-Kentucky area. One of these, *Zygosturmia protoparcis* (Towns) (*Sturmia distincta* Wied. of authors), ranges from Tennessee to Florida (Madden and Chamberlin), Jamaica (Gowdey 1923), Puerto Rico (Catoni 1922), and the Barbados (Bourne 1921). This species attacked *P. sexta* in the United States but was reported from *Agrius cingulatus* (F.) in the Carribean.

Sturmia incompta (V. d. W.) (*inquinata* (Wulp)) has been reported from Tennessee (Gilmore 1938a), Missouri (Garman 1897), and Oregon (Lovett 1915). It attacks both species of hornworms. Gilmore also found *Winthemia quadripustulata* (F.) and *Sarcophaga* spp. on both hornworms. He recorded *Compsilura concinnata* Meig. and *Sturmia* sp. on *P. quinquemaculata*, and *Carcelia amplexa* (Coq.) and *Sarcophaga rapax* Walk. on *P. sexta*. *S. rapax*, *Sarcophaga lambens* Wied. and *Sarcophaga sarracenioides* Ald. attacked *P. sexta* in Florida (Madden and Chamberlin 1945). Allen (quoted by Harned 1925) found *Metavoria orientalis* Towns. on the same species in Mississippi, and Alwood (1898) found *Chaetolyga* sp. on it in Virginia. Garman (1897) said that Howard bred *Sturmia trifida* from *P. sexta* but it also attacked *P. quinquemaculata*. Schaffner and Griswold (1934) listed *Achaetoneura frenchii* Will. from the latter in the Northeastern States. *Agrophylax albincisa* Wied. and *Belvosia bifasciata* (F.) occur on *P. sexta paphus* (Cram.) in Brazil (Guimarães 1925; Barradas 1936). Bruner and Scaramuzza (1936) found *Zygosturmia inca* (Towns.) on *P. sexta jamaicensis* Butler in Cuba.

In the North Carolina studies *Z. protoparcis* and *Winthemia* n. sp. (determined by C. W. Sabrosky) have been reared commonly from *P. sexta*, but no dipterous parasites have been

found on *P. quinquemaculata*. Eggs of these parasites seen in the field were white and firmly attached to the anterior segments of the host. Although eggs were seldom seen except on fifth instars, an occasional hornworm was found that was unable to enter the soil because of the presence of large tachinid larvae. In these cases the eggs must have been deposited when the hornworms were much smaller than the fifth instar. Normally the host entered the soil and the parasites pupated underground.

The preference for large larvae is shown in table 4, which gives observations for 2 years on the weight distribution of parasitized, unparasitized, and pupating hornworms. In 1952 the smallest parasitized larva out of a lot of 23 weighed over 5 grams, whereas nearly one-third of those pupating were smaller than this. Apparently some larvae pupated when they were still too small to be attacked by tachinids. However, in 1953 some very small larvae were attacked. These were collected in a plant bed where the population of hornworms was high. The population of tachinids was also high, as shown by the high percentage of parasitization and the number of eggs laid per hornworm. Under these conditions the flies apparently attacked much smaller hornworms than they did in 1952 when populations were lower. Both species of parasites were reared and identified from the hornworms weighed in 1952 and 1953.

DISEASE

Thaxter (1890) observed a destructive epidemic of a fungus disease of hornworms in Connecticut. Garman (1897) reported hornworms killed by "attacks of the chinch-bug fungus" in the vivarium.

White (1923) described a disease of hornworms obtained from Clarksville, Tennessee. He isolated a motile, rod-shaped bacterium and named it *Bacillus sphingidis*. This organism was cultured in various media and was highly lethal in puncture inoculations of hornworms, cutworms, grasshoppers, and catalpa worms, but oral inoculation killed only 8 out of 66 hornworms. Affected larvae in the field turn black and hang by their prolegs from the leaf. The same or a similar disease was seen by Garman (1897) in Kentucky, Reed (1915) in Georgia, Lovett (1915) in Oregon, and Madden and Chamberlin (1945) in Florida. These authors reported that it was most prevalent during the hottest weather and disappeared after the first of September.

In the studies in North Carolina, a few larvae in every brood have been found dead from what appeared to be disease. Only rarely have they exhibited the typical symptoms of hornworm septicemia. However, microscopic examination of dead larvae has shown some of them to be heavily infected with a highly motile bacterium resembling the causative organism of septicemia. Two specimens collected in July 1953 were examined by S. R. Dutky at the Beltsville Agricultural Research Center, and he reported recovery of bacteria very similar to *Bacillus sphingidis* White. Other dead or ailing larvae examined have shown no obvious bacteria.

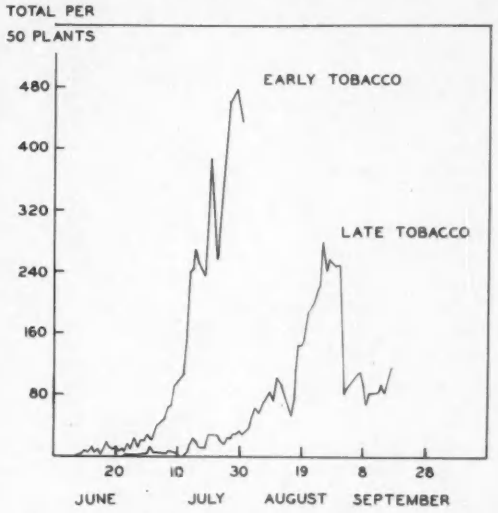


FIG. 1.—Populations of stilt bugs (*Jalysus spinosus*) on tobacco at Oxford, N. C., in 1954.

At Oxford attempts to transmit disease by feeding hornworms on tobacco leaves dipped in suspensions of dead hornworms have given erratic results. For example, on August 5, 1953, 15 hornworms collected in the field were crushed separately in water and pieces of tobacco leaf dipped into the suspensions. Larvae that appeared healthy were fed on these leaves in closed petri dishes. Some larvae died, and these were crushed and the experiment was repeated. Further attempts at transmission gave inconsistent results except in one instance, where disease from two larvae that had died in the original experiment was transferred repeatedly by means of crushed larvae or unwashed dishes. This strain appeared to be highly infective and lethal. Many of the larvae killed had motile bacteria, and Dutky reported that one specimen contained large numbers of a bacterium identical with those seen in field-collected hornworms. He obtained high mortality from these bacteria by puncture inoculation of both species of hornworms, but no mortality above the checks when *P. quinquemaculata* larvae were fed on suspensions.

No major outbreaks of disease were seen in the field during these studies, but C. F. Stahl (personal communication) reported that in 1943, when third-brood larvae were very abundant, large numbers died from a disease resembling

Table 5.—Mortality of hornworm larvae on tobacco plants when caged with predators and in the open, Oxford, N. C.

Predators	Number of plants	Aphids	Number of hornworms	
			July 19	Killed or Missing July 21
		In Cages		
4 Nabids	2	None	8	1
	2	Few to common	8	0
5 Coccinellids	2	None	8	0
	2	Many	8	2
6 Stilt bugs	1	None	4	1
	1	Many	4	0
Totals	12		40	4
		In the Open[a]		
13 Stilt bugs, 2 *Geocoris* sp.	4	None	16	13
13 Stilt bugs, 6 *Geocoris* sp.	4	Few	16	10
10 Stilt bugs, 10 *Geocoris* sp., 4 chrysopids, 3 spiders	4	Common	16	13
8 Stilt bugs, 5 *Geocoris* sp.	4	Many	16	8
Totals	16		64	44

[a]The figures given for the predators are the maximum numbers seen on the plants; numerous coccinellids and one or two nabids, chrosopids, and spiders were found on all plants in the open.

septicemia. It is a common observation that when hornworms are collected or reared for experimental purposes the mortality from disease is likely to be high if the larvae are crowded. Dutky suggested that this may be septicemia transmitted by bites incurred in fighting. Septicemia might also be transmitted in the field by the same means when populations are high.

It is apparent from these observations that hornworm septicemia is endemic in the field and may reach outbreak proportions when populations are high, but it is by no means certain that septicemia is the only disease causing appreciable mortality. Rabb et al. (1957) reported high mortality of *P. sexta* on plants sprayed with spores of *Bacillus thuringiensis* Berliner.

EGG PREDATORS

Gilmore (1938a) said that *Chrysopa rufilabris* Burm., *Geocoris punctipes* (Say), and the stilt bug *Jalysus spinosus* (Say) were egg predators in Tennessee. Madden and Chamberlin (1945) reported that the spider *Peucetia viridans* (Hentz) and the plant bug *Cyrtopeltis modestus* (Dist.) (*varians*) preyed on eggs in Florida.

In North Carolina hornworm eggs observed in the field were frequently attacked by stilt bugs, rarely by various other small Hemiptera. Stilt bugs are common on tobacco, and both adults and nymphs feed on hornworm eggs. The egg shell is often left intact, but partially or completely empty. In 1953 and 1954, when hornworm populations were observed daily, a total of 632 eggs were counted; 150 of these eggs were lost. The losses included 44.7 percent killed by predators, 47.3 percent missing, 1.3 percent lost due to miscellaneous causes, and 6.7 percent that failed to hatch for unknown reasons. Most of the last group were probably injured by predators. Some of the missing eggs may have hatched but disappeared when the larvae were consumed by predators before the next observation. Some eggs were probably brushed off the leaves by men or machines or by the action of wind. Eggs laid on suckers may be lost when these leaves are removed from the plants. However, most of the missing eggs were probably eaten by predators, which may or may not have been stilt bugs.

Stilt bugs are general feeders and have been observed in the field feeding on aphids, newly emerged larvae of *Apanteles*, and various dead insects stuck to the hairs of tobacco leaves. In the laboratory they have been seen feeding on aphid honeydew and on the plant. On July 9, 1953, four bugs under close observation fed on a leaf for appreciable periods. One female spent 37 minutes out of 130 with the beak inserted into plant tissue. However, some animal food appears necessary, as shown by the following experiment:

On July 9 four adult stilt bugs and one nymph were caged on a tobacco leaf with green peach aphids (*Myzus persicae* (Sulz.)). Thirteen days later all the original stilt bugs were alive and had

Table 6.—Wasp activity in small plots infested with hornworms, Oxford, N. C.

Date 1954	Field and Plot	Number of Plants	Observation time	Number of hornworms		Number of wasps seen		
				Total	Killed or Missing	Killing Prey	Feeding on Carcass	Total
July 23	1a	17	10:00 a.m. to 11:50 a.m. 1:50 p.m. to 4:40 p.m.	83	41	8	0	11
26	1b	6	9:45 a.m. to 11:47 a.m.	60	12	6	0	10
	1c	1	1:55 p.m. to 4:50 p.m.	17	15	15	0	27
27	1c	1	8:40 a.m. to 11:50 a.m.	21	11	8	1	28
Aug. 3	2a	15	10:00 a.m. to 7:00 p.m.	32	3	0	0	7
4	2a	15	5:33 a.m. to 6:00 p.m.	28	0	0	0	1
5	2a	15	8:30 a.m. to 5:00 p.m.	30	0	0	0	0
6	2a	15	8:30 a.m. to 11:45 a.m.	30	0	0	0	0
9	2b	15	9:55 a.m. to 5:00 p.m.	33	4	5	3	15
10	3a	15	8:50 a.m. to 4:30 p.m.	30	0	0	0	5
11	2b	15	9:15 a.m. to 4:00 p.m.	33	6	5	1	8
12	3a	15	10:00 a.m. to 3:30 p.m.	26	0	0	0	0
13	2b	15	9:30 a.m. to 4:20 p.m.	30	13	8	2	23
16	3b	60	2:00 p.m. to 4:30 p.m.	22	1	0	0	2
17	2b	15	8:15 a.m. to 4:30 p.m.	33	6	6	0	11
18	3b	60	9:00 a.m. to 4:30 p.m.	19	0	0	0	0
19	2b	15	8:20 a.m. to 4:30 p.m.	33	19	19	4	31
20	3b	60	9:30 a.m. to 4:30 p.m.	10	4	1	0	14
23	2b	15	8:30 a.m. to 4:45 p.m.	33	6	4	1	13
24	2b	15	8:30 a.m. to 4:52 p.m.	31	18	10	4	27

produced an additional seven nymphs. On the same day seven adult bugs were caged with only a leaf for food. Eggs were observed within 24 hours, but no live nymphs were present at the end of 13 days, and six of the original adults were dead.

Tobacco fields seem to be the principal habitat of stilt bugs. On June 24, 1954, a series of sweep samples were taken with a small insect net. In 10 samples of 50 sweeps, made in grass and weeds, only two stilt bugs were taken. On July 12 and 13 a series of 39 similar samples taken on soybeans, beans, cane, corn, clover, cotton, alfalfa, weeds, grass, and brush contained one stilt bug. Sweeps are difficult to take on tobacco plants, but five samples on this crop contained two stilt bugs. In 1954 counts were made of the stilt bugs seen on the plants used for hornworm counts. The results are plotted in figure 1. The highest population was nearly 10 per plant.

PREDATORS OF LARVAE

Garman (1897) reported that skunks (Mustelidae) fed on larvae. Gilmore (1938a) listed wild birds and domestic fowl and the insect predators *Chrysopa rufilabris* Burm., *Calathus opaculus* LeC., and *Polistes* sp. Madden and Chamberlin (1945) listed various birds, the spider *P. viridans*, the plant bug *Cyrtopeltis modestus* (Dist.), and the wasps *Polistes fuscatus* (F.) and *P. metricus* Say. *P. metricus* was said to be active mainly during the early part of the season and was observed to be the chief factor in the control of hornworms in a few open fields of tobacco in Florida. Quaintance (1898) considered *P. bellicosus* Cresson a "great friend to the tobacco grower, as it feeds on the young hornworms and other worms and does much good in this way in Florida." The older identifications in this group of *Polistes* are doubtful. Cuellar (1956) reported that in Panama an assassin bug of the family Reduviidae and wasps similar in appearance to *Polistes* seemed to be chiefly responsible for reducing hornworm populations to the point that a critical evaluation of insecticide treatments could not be made.

Rabb (1950, 1953), working in North Carolina, identified hornworms in the prey brought to the nest by four species of *Polistes*. Hornworms made up 6 to 10 percent of the total prey of three species.

Soon after the studies were begun at Oxford, it was evident that most of the hornworms kept under observation simply disappeared without trace. In 1953, for example, out of 374 larvae marked and observed at 24-hour intervals, 0.8 percent were lost from miscellaneous causes, 2.9 percent entered the soil to pupate, 0.3 percent were parasitized by tachinids, 9.4 percent were found dead and presumed to be diseased, 5.9 percent were killed by predators, 13.9 percent were parasitized by *Apanteles*, and 66.8 percent were missing. Since precautions were taken to prevent movement to other plants, it could be assumed that most of the missing larvae were

Table 7.—Number of wasp flights and number of hornworms killed by four species of *Polistes* in observation fields, August 9–24, 1954, Oxford, N. C.

Species	Number of flights			Number of hornworms killed		
	Field 1	Field 2	Field 3	Field 1	Field 2	Field 3
exclamans Vier.[a]	5	87	1	5	35	0
fuscatus (F.)	65	49	9	30	22	0
rubiginosus Lep.	1	0	0	1	—	—
annularis (L.)	0	0	9	—	—	1

[a]In some cases *exclamans* may have been confused with *hunteri* Bequaert.

carried away by unidentified predators. *Polistes* wasps were commonly seen killing hornworms in the field, and Rabb (1953) showed that the wasps killed large numbers of third- and fourth-instar larvae but found only a few second instars and no firsts in prey brought to the nest. Since the field data showed heavy losses in the first and second instars as well as in the third and fourth, a search was begun for the predators responsible for losses in the early instars.

The predators that might kill hornworms and that are fairly common in tobacco fields are spiders, carabids, stilt bugs, nabids, *Geocoris* sp., chrysopids, coccinellids, yellow jackets (*Vespula* sp.), and *Polistes* spp.

Most of the spiders on tobacco are so small that it is unlikely that they would attack hornworms. *P. viridans* has been seen feeding on hornworms, but is too scarce in North Carolina to account for more than a small fraction of the losses.

Carabids are seldom seen on the plants during the day, but might kill hornworms at night. To check this, on July 28, 1953, counts were made at dawn and dusk. There were 58 eggs and larvae on 50 plants. One died and one was missing in three successive nights. One died, three were killed by predators, and 12 were missing during daylight hours. In a 24-hour period on August 5–6, 5 larvae out of 29 were missing during the day and none disappeared at night.

Yellow jackets are sometimes seen in tobacco fields, and in October 1955 were seen feeding on dead hornworms in a third-brood population. When live third- and fourth-instar larvae were placed on the same leaf where yellow jackets had been feeding, they were killed and carried away, a small piece at a time. Since this was the only time these predators were observed attacking hornworms, they are probably of little importance.

When small predators were caged in the laboratory, nabids, stilt bugs, and coccinellids killed small hornworms when no other animal food was available. The nabids were particularly voracious, but ignored hornworms when aphids were present.

In July 1954 a field experiment was set up in which some larvae were caged with the small predators and others placed on marked plants in the open where these predators were also present. Cloth bags covering four or five leaves at the top of each plant were used as cages. Some of the plants in the cages and some in the open were infested with aphids and some were not. There were also a few dead flies and small Hymenoptera present that had been trapped on the sticky hairs of the plants. First-instar hornworms were placed on each plant on July 19.

Table 8.—Emergence of *Protoparce sexta* moths from hibernation cages, 1936–43[a]

Year	Number of larvae entering soil	Percent emerged
1936	3936	8.8
1937	2312	19.6
1938	1504	6.5
1939	1997	11.6
1940	1705	18.8
1941	1400	20.7
1943	1500	23.8
Total or weighted mean	14,354	14.8

[a]From unpublished reports by W. A. Shands and C. F. Stahl, both formerly of the Oxford, N. C., laboratory.

All but two of the survivors in the cages and two in the open had changed to the second instar by July 21. The results of this experiment are given in table 5. In the cages with the predators, hornworm mortality was very low whether or not aphids were present. In the open, mortality was high but there was no apparent correlation with either the number of predators or the number of aphids. It is quite clear that, although the small resident predators may have killed a few hornworms, these enemies did not account for most of the losses.

Since the predators resident on the tobacco plants did not destroy the hornworms, the only reasonable explanation for their rapid disappearance is that wasps or other nonresident predators

carried them away. Observations were then made of wasp activity on small plots of tobacco infested by hand with hornworms collected elsewhere. Table 6 gives the results of a long series of observations in several fields. The total number of hornworms was determined by counts

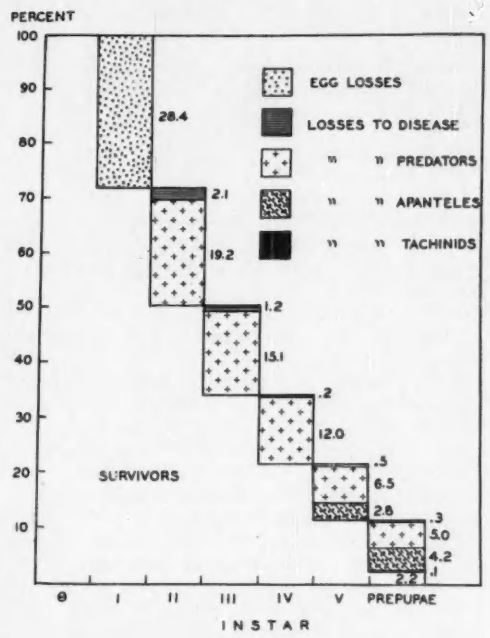


FIG. 2.—Mean losses of hornworms to natural enemies in North Carolina, 1953–56, based on initial populations.

made at the beginning, and the number lost by counts at the end of each period of observation. The total number of wasps seen generally exceeded the number taking prey, because many of them flew through the plot or searched the plants without finding prey. Occasionally a budworm was killed.

The first observations, on July 23, were made from the top of a tall stepladder placed about 20 feet away from a plot of 17 plants and partially concealed by trees. In 4 hours and 40 minutes, 8 hornworms were killed by wasps, but 33 disappeared without trace. On July 26 the size of the plot was reduced to six plants. Wasps were seen to take six hornworms, but this was still only half the losses. Accordingly 17 larvae, most of them in the second instar, were placed on a single plant, and the observer sat on the ground under it. Fifteen larvae were lost, all killed by wasps. The same technic was used again the next day, and 8 out of 11 hornworms lost were killed by wasps. Seven of these hornworms were in the first instar. The wasps usually ate these small larvae on the spot, and only rarely carried anything away. This explained why Rabb had found so few small hornworms in food pellets brought to the nest by *Polistes*. Occasionally a wasp bit a hornworm and inflicted a mortal wound but did not eat it. Some of the victims were eaten later by the same or other individuals. Later observations established that such behavior by wasps is common. Hornworms of any size are frequently killed and abandoned, or they may be carried about for a few minutes and then dropped (Rabb and Lawson 1957). Many wasps searched the plant without finding a victim, and a few were seen to examine a hornworm without injuring it. Most of the wasps seen were *P. fuscatus* (F.) and a few were *P. exclamans* Vier.

Although the observations made on single plants established the fact that *Polistes* preys on first- and second-instar hornworms, they did not prove that these predators are of any great importance under natural conditions. The observed losses were abnormally high, and several colonies of *Polistes* were located nearby in artificial shelters.

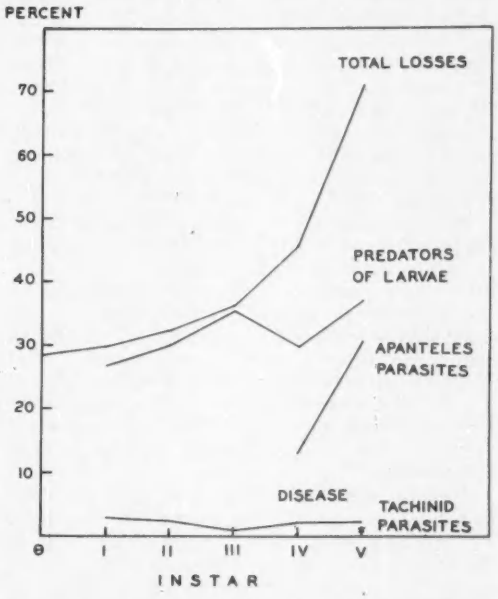


FIG. 3.—Hornworm mortality in North Carolina, 1953–56, based on the population reaching each instar.

In order to continue the work in a more normal situation, on August 3 an observation plot was set up in another field (plot a, field 2), where natural populations of both hornworms and wasps were present. However, it was still necessary to increase the infestations in the plot artificially, because only two or three larvae would ordinarily be found in so small an area.

Table 9.—Emergence of *Protoparce sexta* moths from cages placed in different soil types.[a]

1943			1945		
Soil type	Total number of larvae	Percent emergence	Soil type	Total number of larvae	Percent emergence
Sandy	500	5.0	Sandy	175	28.6
Sandy Loam	500	4.6	Medium	200	13.5
Red clay	500	59.6	Medium heavy	173	8.1
			Heavy	168	2.4
			Heavy clay	171	1.2

[a]From reports by C. F. Stahl, formerly of the Oxford, N. C., laboratory.

The hornworms varied from the first to the fifth instar.

During the first few days of observation on this plot very few hornworms were lost. At this time the natural population of hornworms was low and few wasps were seen hunting them. On August 9 a plot was set up at the end of the field (2b), and on the next day another plot was established in a different field (3) about a mile away. This field had been arranged in randomized blocks for agronomic experiments and was composed of plots of tobacco in different stages of maturity. Old plants had few hornworms, but young plants had many. The first observation plot (a) established in field 3 consisted of old plants artificially infested. Later observations (b) were made on young plants with a natural infestation.

In this series of experiments (August 3–24) the observer sat on top of a tall stepladder placed as near the plants as possible. From this position he could look down on the plants but could not see all the hornworms. Consequently, some losses were not observed, but out of 80 hornworms lost 58 were killed by wasps. Furthermore, in the whole series of observations there is a very close correlation ($r=0.934$) between total losses and wasp predation. The only hornworm predators of any significance in these plots were *Polistes* wasps.

To rule out the possibility that birds were also important predators, hornworms in the plots were counted every morning and evening for 10 days in field 2, and for 9 days in field 3, but a watch was kept only on alternate days. In field 2, where the average time between counts was 7 hours and 25 minutes, the mean loss per day was 32.0 percent during the 5 days an observer was present. When the observer was absent, the average time was 7 hours and 37 minutes and the loss was 16.1 percent. Losses were invariably higher on days when a watch was kept, and the mean loss was about twice as great. This is the opposite of what might be expected if predation by birds was a significant factor. Apparently the mere presence of the observer increased the kill by predators. In field 3 an observer was present 5 days; the average time between counts was 6 hours and 32 minutes, and the mean loss was 10.7 percent. On the 4 days the observer was absent the average time was 8 hours and 16 minutes and the mean loss 13.3 percent.

It is possible that the tall stepladder, which was moved from field to field, or the observer himself, provided a landmark for wasps returning to the plot after making a kill. It is known that some individuals did return repeatedly. For example, on July 27 between 2:37 and 4:37 p. m., a marked *P. fuscatus* visited a plot five times, killed three hornworms, took another from a *P. exclamans*, and carried off part of a carcass left on a previous visit. On August 24 between 9:44 a. m. and 4:36 p. m., a marked *P. exclamans* made 19 visits to plot 2b, killed 10 hornworms, and carried away four pellets from carcasses previously killed. At field 2 the ladder was a conspicuous landmark in the open, but at field 3 there were trees nearby. This may be the reason for the difference between locations.

The data give no indication that birds were a significant cause of hornworm losses. Except for an occasional larva killed by disease or green spiders, all the larvae whose death was witnessed were taken by wasps. These results agree with the less detailed observations of four persons who in the last 5 years have each spent hundreds of hours in tobacco fields scattered over the State. Wasps are frequently seen where hornworms are present and are nearly always numerous when populations of the host are high. These predators have ruined many control experiments by carrying off the larvae used in artificial infestations or by destroying the populations remaining in the checks after treatment. Birds, except hummingbirds feeding on open flowers, are not often seen in tobacco fields. Occasionally crows, blackbirds, or starlings may descend on fields heavily infested with large hornworms, but records of such occurrences are rare.

The conclusion that *Polistes* wasps are the primary predators of hornworms is supported by

Table 10.—Parasitization by *Apanteles congregatus* of field-collected hornworms reared in the laboratory compared with larvae remaining in the field and subjected to attack by other enemies, Oxford, N. C.

Year	Brood	Reared in laboratory		Observed in field		Indicated loss of parasitized larvae (percent)
		Number of hornworms	Percent parasitized	Number of hornworms	Percent parasitized	
1953	3	48	77.1	124	39.5	49.0
1954	2	52	88.5	42	33.3	62.2
	3	91	96.7	43	14.0	85.7

certain control experiments conducted in 1955 and 1956. It was discovered in 1954 that *Polistes* would nest in wooden boxes put up on trees and posts. In 1955, 18 of these artificial shelters were put around the edges of each of five tobacco fields located at least 10 miles apart from the central part of the State northward. Five fields on the same farms were used as checks. In 1956 this experiment was repeated on three paired fields in Columbus County in the southern part of the State, one in the central portion, and one at Oxford in the north. Since two broods of hornworms occurred on the harvestable leaves each year, there were 20 populations of eggs laid on 10 check fields and the same number on the protected fields. In the checks six populations produced outbreaks of large hornworms that would have justified insecticide treatment, but in the protected fields only one such outbreak occurred.

Four species of *Polistes* were seen in the fields where observations were made in 1954. The number of times each species was seen and the number of hornworms killed are given in table 7. Differences between fields were probably due to habitat. *P. annularis*, which prefers forested areas (Rabb 1953), was found only at field 3, which was surrounded by woods; *P. fuscatus*, which hunts in brush and open fields, was most abundant at field 1, which had woods on one side; *P. exclamans*, which hunts in open fields, occurred mostly in field 2, which was some distance from trees. Two additional species, *P. metricus* Say and *P. hunteri* Bequaert, have been seen preying on hornworms. *P. bellicosus* Cresson nested in artificial shelters adjacent to tobacco fields in Columbus County in 1956, but has not been observed attacking hornworms. Table 7 indicates that *P. annularis* and *P. rubiginosus* were much less abundant than *P. fuscatus* or *P. exclamans*. Wherever observations have been made in the state, the last two species have always been far more common than any others. According to Rabb (1950), the seven species mentioned above are the only *Polistes* recorded from the area of study.

Table 6 shows great variations in wasp predation and in hornworm losses from day to day. These variations were not associated with any obvious changes in weather, and the cause of the fluctuation is unknown. Rabb and Lawson (1957), in a study of factors influencing wasp predation, found that the proportion of hornworms brought to the nest decreased sharply with its distance from the tobacco field and was further reduced by the presence of other prey species.

ENEMIES OF PUPAE

The tachinid flies are primarily enemies of the prepupal and pupal stages since, although they oviposit on the larvae, most of their life is spent underground. Garman (1897) considered skunks important predators on hornworm pupae. Gilmore (1938a) and Madden and Chamberlin (1945) reported that skunks and moles destroyed large numbers. Gilmore also listed "lampyrid larvae, *Megaselia nigriceps* (Loew.)" under predators of pupae, but since this genus is listed in catalogues as a phorid the identification is doubtful.

Pupal survival in cages out-of-doors has been studied by various investigators. Gilmore reported that at Clarksville, Tennessee, moth emergence was 24.3 percent of the *P. sexta* and 4.8 percent of the *P. quinquemaculata* that entered the soil. Madden and Chamberlin found 20–53 percent emergence of *sexta* in Florida.

The results of studies at Oxford are summarized in tables 8 and 9. Larvae were collected in September and allowed to enter the soil in large cages. The survival varied from year to year. In 1943 it was much higher in a clay soil than in sand, but in 1945 much lower. These contradictory results indicate that some factor other than soil type was responsible. This factor could well have been some unidentified enemy. The crowding of larvae in pails or tubs when they are collected or in the cages before they enter the soil would be conducive to the spread of disease. Disease is nearly always present in the field, and

Table 11.—Multiparasitism of fifth-instar hornworms collected in tobacco fields in North Carolina, 1952.

Locality	Date of collection	Total number	Number parasitized by		
			Apanteles only	Tachinids only	Both *Apanteles* and Tachinids
Oxford	Sept. 2	22	9	1	9
Wilton	Sept. 4	20	10	2	0
Zebulon	Sept. 17	20	16	0	2
Wilson	Sept. 17	20	15	0	2
Williamsboro	Oct. 21	52	28	3	9

some larvae always died before they entered the ground in these experiments.

It is concluded that during their life in the soil hornworms are killed by parasites whose eggs are deposited on the larvae, by diseases which may or may not be acquired in the larval stage, and by various predators. The effects of these enemies on pupal survival have not been measured.

EFFECT OF WEATHER AND CULTURAL FACTORS ON HORNWORM MORTALITY

Madden and Chamberlin (1945) showed that hornworm development was affected by temperature, and indicated that high humidity favors disease. In the Oxford investigations, which were concerned mostly with the larval stage, there has been no evidence that hornworms were killed by weather conditions except that violent wind and rain might have washed a few eggs or small larvae off the plants. The effects of weather on host plants may be of more importance. Since the number of eggs laid is affected by the vigor and succulence of the plants, drought or high temperatures may reduce the number laid in any particular field. In the fall of 1952 frost killed tobacco plants while a few larvae were still present. It is possible that, in years when the third brood is delayed, early frosts might thus destroy much of the overwintering brood. There was no evidence that the larvae themselves were killed by cold. Workers engaged in removing tops and suckers from tobacco plants usually kill any hornworms seen, and many are thrown on the ground with the discarded leaves.

According to Gilmore (1938a), repeated experiments in Tennessee have shown that over 90 percent of the hornworm pupae can be killed by normal fall and winter plowing. He said that the pupal cell is formed at a depth of 4–7 inches. Madden and Chamberlin measured the depth of pupation of nearly 1500 larvae in undisturbed red clay soil, and found it to range from 1½ to 9½ inches, with a mean of 5½ inches. In limited experiments at Oxford, where the soil had been dug up a short time prior to use, pupation generally occurred at the bottom of the cage, or where firm soil was encountered by the burrowing larvae.

The average depth of pupation, as recorded by Gilmore and by Madden and Chamberlin, would be at about the average depth of plowing. Thus, burrowing larvae probably form a cell when they encounter the hard soil of the plow sole. When the land is plowed again, some pupae in this position are found to be ruptured by the plowshare. Most of the cells above plow depth are destroyed so that the naked pupae are in contact with the soil on all sides instead of lying free in a roomy cell. This may increase pupal mortality or affect the ability of the moth to dig out of the soil. Plowing might also expose some pupae to weather and to predators.

Gilmore (1938a) suggested that drought prevents emergence. Farmers maintain that hornworm broods appear when the moon is bright. Madden and Chamberlin found no relation between oviposition and moonlight. Stahl kept records (unpublished) of moth catches in traps for 12 years at Oxford, and found no relation between catches and rainfall or the phases of the moon.

In brief, cultural operations cause hornworm mortality. Weather affects populations indirectly through the host plants, but there is no conclusive evidence that weather kills hornworms directly or by preventing emergence of the moth.

RELATIONSHIPS BETWEEN ENEMIES OF HORNWORMS

The two species of *Protoparce* that attack tobacco in North Carolina are far more abundant than other sphingids. The food supply of the parasties that depend on this family is therefore greatly affected by the abundance of hornworms, which in turn is much reduced by other enemies. For example, the mean hornworm survival to the prepupal stage is about 2 percent of the number of eggs laid; most of the other 98 percent are killed by predators. Since the tachinids usually attack hornworms just before they enter the soil, the population of these parasites must be greatly affected by this high mortality. The

Table 12.—Percent hornworm mortality, summarized by broods, years, and localities.

	Number of hornworms	Eggs lost	Larvae killed by predators or missing	Larvae dead presumably diseased	Parasitized by *A panteles*	Parasitized by tachinids	Miscellaneous losses	Survival to prepupae
			Summary by broods, mean 1952–54, Oxford only					
1	187	27.1	64.6	4.3	0	1.2	1.1	1.7
2	259	18.1	63.6	6.9	8.6	0.5	0	2.3
3	238	31.5	34.1	8.4	23.1	0	0.4	2.5
			Summary by years, broods 1 and 2, Oxford only					
1952	270	43.7	33.6	5.4	6.3	1.6	0	9.4
1953	313	19.5	70.6	6.4	1.0	0.3	0	2.2
1954	75	18.7	56.0	4.0	20.0	1.3	0	0
1955	35	25.7	42.9	5.7	17.1	2.9	0	5.7
1956	46	32.6	47.8	6.5	10.9	0	0	2.2
			Summary by localities, broods 1 and 2					
1955								
Youngsville								
Rolesville	269	43.1	53.2	1.1	0.7	0	0	1.9
McCullers	80	37.5	42.5	3.8	12.5	0	0	3.7
Greenville	72	36.1	59.7	1.4	2.8	0	0	0
Selma	64	39.1	53.1	1.6	6.2	0	0	0
1956								
Clayton	322	20.8	59.9	2.5	3.1	0	1.0	12.7
Columbus County	62	30.6	69.4	0	0	0	0	0

predators, which feed on many other hosts and are thus much less dependent on the hornworms, are probably not greatly influenced by competition with hornworm parasites.

In addition to these indirect effects, there is also severe direct competition between enemies. In the discussion of parasites it was noted that *A panteles* eggs are deposited in first- to third-instar hornworms but emergence occurs in the fourth and fifth instars. During the period of parasite development the hornworms are subject to heavy predation by wasps. Wasps apparently make no distinction between parasitized and normal larvae. Rabb (1953) found *A panteles* larvae in hornworms brought to the nest by *Polistes*. Table 10 compares the parasitization of hornworms in the field near Oxford with others collected in the field, but reared in the laboratory. Laboratory-reared larvae were in the second and third instars when collected. The number observed in the field was the total number of first instars seen. The figures for the indicated loss of parasitized larvae are equal to $\frac{100(NP - F)}{NP}$ where N is the total number of hornworms observed in the field, F the number parasitized in the field, and P the percent parasitization in the laboratory. Parasitization was high in laboratory-reared larvae, yet few parasites emerged in the field. The difference was due to predation. Half or more of the parasitized larvae were killed by predators.

Hornworms parasitized by tachinids may be destroyed by either predators or *A panteles*. Such direct competition is probably less important than a reduction in the food supply, because tachinids prefer to oviposit on large hornworms. Mature larvae are avoided by *Polistes*, and not many hornworms reach this size if they are parasitized by *A panteles*. However, when both *A panteles* and tachinids are abundant, there may be considerable overlapping (table 11). When tachinid eggs are deposited on a hornworm already parasitized by *A panteles*, the braconid will emerge and the tachinids will perish.

Table 12 compares hornworm mortality in different broods, years, and localities. At McCullers and at Oxford from 1953 to 1955, fifth instars entering the ground were trapped. At all other localities larvae surviving 4 days or more in the fifth instar were assumed to have entered the soil. The survival figure for Clayton is almost certainly too high. There is apparently a reduction in egg losses in the second brood. Losses to predators are about the same in the first two broods, but there is a definite reduction in the third. This third brood appears in September and October, at a time when brood rearing by wasps has begun to decline or has stopped.

Disease and parasitization by *A panteles* increase as the season advances. Although no parasitized first-brood larvae were found in the samples, actually there is always some parasitization in this brood, but very little. The sharp increase in the third brood is partly a reflection of the

decrease in predation; that is, the more larvae the predators leave, the more parasites can emerge. Table 12 indicates that parasitism by tachinids declined with the season, but the percentages were so low that these figures mean little. The number of larvae surviving attack by all enemies increased as the season advanced. There was considerable variation from year to year and place to place in the percentage kill by all enemies, but the proportions killed by different enemies were similar in all years and at all localities. Except in 1952, the greatest loss was always in the number killed by predators or missing. The next highest loss occurred in the egg stage, except at Oxford in 1954, when the kill by *Apanteles* was slightly greater. This parasite occasionally took a significant fraction of the host population, but losses to disease and tachinids were always low.

EFFECT OF ENEMIES ON POPULATIONS

The mean losses occurring in 1,661 hornworms that were found in the egg stage and observed until they entered the ground or died are given in figures 2 and 3. The data include 37 different populations from 1953 to 1956. The dominant influence of the predators of larvae is clearly shown. These enemies kill more hornworms than all others combined, although egg predators and *Apanteles* take appreciable portions.

Figure 2 indicates that the percentages lost to disease and predators decline as the size of the hornworms increases. This does not mean that hornworms become less susceptible to these enemies as they grow larger, but merely that they become less numerous. If the percentage losses are based on the number of larvae entering each instar, as in figure 3, instead of the number of eggs laid, as in figure 2, the losses to disease are nearly the same in every instar and losses to predators increase as the hornworms grow larger, except in the fourth instar. The rise in the fifth instar means very little, since the numbers were small. In other words, hornworms of all sizes are equally susceptible to disease and become more attractive to predators as they grow larger until they reach the fourth and possibly the fifth instars. Losses to parasites begin in the fourth instar, when *Apanteles* first emerges, and increase sharply in the fifth. Total losses to all enemies show a smooth curve which tends to increase exponentially.

It is apparent that the natural enemies have a pronounced effect on hornworm populations. Even under the most favorable conditions the number surviving the egg and larval stages did not greatly exceed 10 percent (table 12, Oxford 1952 and Clayton 1956), and in some populations it was zero. Although the hornworms are important pests of the tobacco crop, damaging populations do not occur every year in all fields. Some localities are relatively free from damage, and even the worst areas sometimes have low populations. About 80 percent of the tobacco eaten by hornworms is consumed by fifth instars. Since most of them die before they reach this instar, it is obvious that the enemies reduce crop losses.

REFERENCES CITED

Alwood, W. B. 1898. On the life history of *Protoparce carolina*. (Abstract; in Proc. 10th Ann. Meetg. Assoc. Econ. Ent.) U. S. Dept. Agric., Div. Ent. Bull. (n.s.) 17: 72–74.

Ashmead, W. H. 1887. Report on insects injurious to garden crops in Florida. U. S. Dept. Agric., Div. Ent. Bull. 14: 9–28.

Barradas, H. 1936. Uma lagarta do Tabaco. O Campo [Rio de Janeiro] 7(77): 30.

Bourne, B. A. 1921. Report of the Assistant Director of Agriculture on the Entomological and mycological work carried out during the season under review. Barbados. Rept. Dept. Agric. 1919–20: 10–31.

Bruner, S. C., and **L. C. Scaramuzza.** 1936. Reseña de los insectos del tabaco en Cuba. Estac. Exptl. Agron. Santiago de las Vegas. Circ. 80. 51 pp.

Catoni, L. A. 1922. Plagas de insectos que atacan a las plantaciones de batata. Rev. Agric. Puerto Rico 9(3): 25–28.

Cuellar, R. 1956. La Mosca chupadora y el gusano cornudo del tabaco. Inst. Nac. Agric. [Divisa, Rep. Panamá] Fol. 25. 10 pp.

de Azevedo, A. 1924. A lagarta "verde" do fumo. Correio-Agric. [Bahia] 2(12): 361–3.

Fulton, B. B. 1940. The hornworm parasite, *Apanteles congregatus* (Say), and the hyperparasite, *Hypopteromalus tabacum* (Fitch). Ann. Ent. Soc. America 33(2): 231–44.

Gahan, A. B. 1930. Synonymical and descriptive notes on parasitic Hymenoptera. Proc. U. S. Natl. Mus. 77, Art. 8 (2831). 12 pp.

Garman, H. 1897. Notes on tabacco worms, from observations made in 1896. Kentucky Agric. Expt. Sta. Bull. 66: 6–32.

Gilmore, J. U. 1938a. Observations on the hornworms attacking tobacco in Tennessee and Kentucky. Jour. Econ. Ent. 31(6): 706–12.

1938b. Notes on *Apanteles congregatus* (Say) as a parasite of tobacco hornworms. Ibid. 712–5.

Gowdey, C. C. 1923. The principal insect pests of tobacco in Jamaica. Jamaica Dept. Agric. Ent. Circ. 9. 6 pp.

1925. Report of government entomologist. Jamaica. Ann. Rept. Dept. Sci. and Agric. 1924: 17–20.

Guimarães, J. S. 1925. Lagartas inimigas do fumo na Bahia. Chacaras e Quintaes [São Paulo] 31(1): 23–25.

Harned, R. W. 1925. Annual Report of the Zoology and Entomology Department. Mississippi Agric. Expt. Sta. 37th Ann. Rept. 1923–24: 24–28.

Kuitert, L. C., and **A. N. Tissot.** 1956. Insect pests of flue-cured tobacco and their control. Florida Agric. Expt. Sta. Bull. 573. 34 pp.

Lovett, A. L. 1915. The tomato worms, *Phlegethontius sexta*, Johan., *Phlegethontius quinquemaculata*, Haw Oregon Agric. Expt. Sta., Second Biennial Crop Pest and Hortic. Rept., 1913–14: 170–2.

Madden, A. H., and **F. S. Chamberlin.** 1945. Biology of the tobacco hornworm in the southern cigar-tobacco district. U. S. Dept. Agric. Tech. Bull. 896. 51 pp.

Metcalf, Z. P. 1909. Insect enemies of tobacco. North Carolina Dept. Agric. Spec. Bull. 70 pp.

Muesbeck, C. F. W. 1921. A revision of the North American species of ichneumon-flies belonging to the genus *Apanteles*. Proc. U. S. Natl. Mus. [1920] 58(2349): 483–576.

Muesbeck, C. F. W., K. V. Krombein, H. K. Townes, et al. 1951. Hymenoptera of America north of Mexico. Synoptic catalog. U. S. Dept. Agric. Monogr. 2. 1420 pp.

Peluffo, A. T. 1923. Enemigos del tabaco. Uruguay. Minist. Indust., Defensa Agric. Bol. Mens. 4(11–12): 125–8.

Porter, C. E. 1918. Materiales para la entomlogía económica de Chile. Anal. Zool. Aplic. 5(1): 3133.

1920. Sobre dos bracónidos argentinos. Rev. Chilena Hist. Nat. 24(2–4): 33–34.

Quaintance, A. L. 1898. A preliminary report upon the insect enemies of tobacco in Florida. Florida Agric. Expt. Sta. Bull. 48: 154–88.

Rabb, R. L. 1950. A contribution to the ecology of *Polistes* in North Carolina. M.S. Thesis, North Carolina State College, Raleigh.

1953. Observations on the predatory activities of *Polistes annularis* (Linnaeus), *P. f. fuscatus* (Fabricius), and *P. e. exclamans* Viereck (Hymenoptera: Vespidae). Ph.D. Thesis, North Carolina State College.

Rabb, R. L., and **F. R. Lawson.** 1957. Some factors influencing the predation of *Polistes* wasps on the tobacco hornworm. Jour. Econ. Ent. 50(6): 778–84.

Rabb, R. L., E. A. Steinhaus, and **F. E. Guthrie.** 1957. Preliminary tests using *Bacillus thuringiensis* against hornworms. Jour. Econ. Ent. 50(3): 259–63.

Reed, W. V. 1915. Some of the more important truck crop pests in Georgia. Georgia State Bd. Ent. Bull. 41. 39 pp. (Tomato hornworms, pp. 24–27.)

Schaffner, J. V., and **C. L. Griswold.** 1934. Macrolepidoptera and their parasites reared from field collections in the north-eastern part of the United States. U. S. Dept. Agric. Misc. Publ. 188. 160 pp.

Thaxter, R. 1890. Report of the mycologist. Connecticut Agric. Expt. Sta. Rept. 1890: 80–113.

Thompson, W. R. (ed.). 1946. A catalogue of the parasites and predators of insect pests. Section 1. Parasite host catalogue. Part 8. Parasites of the Lepidoptera (N–P; pp. 386–523). Belleville, Ontario: Imperial Parasite Service.

White, G. F. 1923. Hornworm septicemia. Jour. Agric. Res. 26(10): 477–86.

Wirth, W. W. 1956. New species and records of biting midges parasitic on insects (Diptera, Heleidae). Ann. Ent. Soc. America 49(4): 356–64.

Wolcott, G. N. 1922. Los gusanos de la hoja del tabaco. Puerto Rico Insular Expt. Sta. Circ. 53. 15 pp.

THE FLIGHT ACTIVITIES OF DOLICHODERUS (HYPOCLINEA) TASCHENBERGI (HYMENOPTERA: FORMICIDAE)[1]

PAUL B. KANNOWSKI

Department of Biology, University of North Dakota, Grand Forks

ABSTRACT

Nuptial flights were observed at a nest on the Edwin S. George Reserve, Livingston County, Michigan, between June 17 and July 28, 1957; they took place daily except when inclement weather occurred during the flight period. Flights occurred between approximately 20 minutes before sunrise and 4 hours after sunrise; at temperatures of 58° F. or higher; at low wind velocities; at high relative humidities (80%–99%); and under various sky conditions. The time of the morning of the emergence of the alates from the nest and of the beginning of flights was influenced by the temperature. The alates flew from the vegetation near the nest. Prior to flight each alate usually fluttered its wings while holding on to the vegetation; it became airborne by releasing its hold while fluttering. The alates usually flew toward open areas at angles of 30° to 60° from the horizontal; their flight speed varied from 2 to 5 feet per second. Flights were moderate in size, usually comprising 300–400 alates. The daily flight duration averaged 66 minutes. After the day's flight was over, a small number of alates came out of the nest and paraded over the nest surface. This behavior occurred throughout the day and, on warm evenings, during the night. These flights are compared to those of the closely related species, *D. mariae*.

According to Creighton (1950), the ant genus *Dolichoderus*[2] is represented in North America by four species: *mariae* Forel, *plagiatus* (Mayr), *pustulatus* Mayr, and *taschenbergi* (Mayr). All occur on the Edwin S. George Reserve, Livingston County, Michigan. The flight activities from colonies on the George Reserve have recently been described for three of these species: *D. mariae* by Talbot (1956) and Kannowski (1959), and *D. plagiatus* and *D. pustulatus* by Kannowski (op. cit.). In the summer of 1957, at the George Reserve, I observed the flights of the fourth species, *D. taschenbergi*. Hence, *Dolichoderus* becomes the first ant genus for which significant features of the flight activities of all North American species are known. Because all of these flight activities were observed at the same locality, comparison of the behavior of the several species should help indicate which features are innate and which are environmentally controlled. Future observations of *Dolichoderus* flights at other localities should provide additional information especially on adaptation to diverse environmental conditions.

Only two colonies of *D. taschenbergi* are known to occur on the George Reserve. I found the first colony on May 19, 1956; the other colony was discovered about 1200 feet distant by Mary

[1]Accepted for publication April 2, 1959.

[2]Brown (1950, p. 249) suggested that *Hypoclinea* should be raised to the rank of genus but did not give the bases for his decision. Until his opinions are substantiated, it seems preferable to maintain the usage of Creighton (op. cit.).

Talbot on July 14, 1957. Miss Talbot and I watched several flights from the first colony in July 1956. During May and June 1957 I observed this same colony at intervals of approximately 1 week to check the brood development. In 1957 the first alates were discovered in the nest on June 8; these were males. The first flight observed took place on June 17. However, no observations were made between June 11 and 15; hence, one or more flights may have taken place before June 17. From June 26 to August 1, 1957, this colony was under continuous observation; 30 additional flights were observed between June 26 and July 28, after which date no alates were seen. My observations of these flights are presented below, and unless otherwise stated are based upon the observations made in 1957 at the first colony.

ACKNOWLEDGMENTS

The facilities at the Edwin S. George Reserve of the University of Michigan were kindly made available by T. H. Hubbell, Director, and I. J. Cantrall, Curator. I also wish to thank Mary Talbot, Lindenwood College, and H. K. Wallace, University of Florida, for their assistance.

METHODS

I visited the nest each morning during the flight season, attempting to arrive before the alates emerged from the nest and then following their actions until the last alate had flown on that day. Frequently, however, the alates had emerged by the time I arrived, and several times the flights were already in progress.

Records were kept of the climatic conditions, mainly at the time of emergence from the nest, at the beginning of flights, and at the end of flights. Temperatures were recorded at a level of 10 cm. above the ground surface using a mercury bulb thermometer; occasionally temperatures within the nest itself were obtained, by means of a Weston dial-type thermometer. Relative humidity readings were also taken at approximately 10 cm. above the ground surface, using a Serdex meter and a sling psychrometer. Sky conditions were recorded as clear, partly cloudy, cloudy, overcast, or fog. The light reflected from the surface of the nest was measured with a Weston photographic light meter and recorded in candles per square foot. Nine readings were obtained, each taken at a different position on the nest; these were averaged to give a single mean record of the illumination. Wind velocity was not measured, but estimates were recorded as calm, slight, moderate, or strong. The size of the flight population was estimated on the basis of partial counts of the alates on the vegetation prior to flight, and also on the basis of 2-minute-long counts of the number of alates taking flight, recorded at random five or six times during the flight. The flight activities terminology used herein is based upon Kannowski (op. cit.).

HABITAT

The colony under observation had built its nest in an ecotone between a second-growth oak and aspen woods and an abandoned field (ESGR Grid 0–5). The nest was largely shaded by adjacent vegetation except toward the southeast, in which direction the field lay. The principal trees were black oak (*Quercus velutina* Lam.) and quaking aspen (*Populus tremuloides* Michx.). Young saplings of these two species were frequent near the nest, and the *D. taschenbergi* workers were tending aphids [*Periphyllus bruneri* (Wms.), det. L. M. Russell] on the young branches, especially of the aspens[3]. The ground surface near the nest was occupied mainly by blackberries (*Rubus* sp.) and Canada bluegrass (*Poa compressa* L.). Bracken [*Pteridium aquilinum* (L.) Kuhn] was the only other plant that was frequent near the nest. Colony No. 1 occupied the same nest from May 1956 to August 1958, whereas the second colony moved into a new nest about 15 feet from the old one between August 1957 and August 1958.

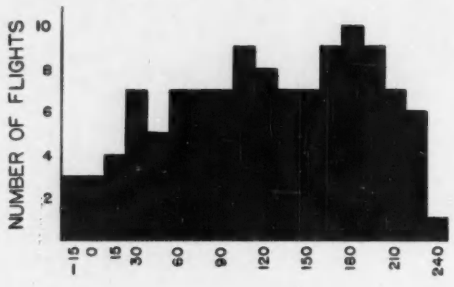


FIG. 1.—Frequency histogram of the occurrence of flights during the early morning hours, based on 15-minute intervals.

The nest construction was similar to that described by Wheeler (1905) for *D. taschenbergi* and by Talbot (op. cit.) for *D. mariae*. The nest was scarcely noticeable among the grass and leaves on the ground. Its surface was a slightly arched roof, about 18 cm. in diameter and rising about 5 cm. above the ground at the center. This roof was composed of tiny bits of stems and leaves, mainly of grasses, which were formed into a layer 5 to 8 mm. thick, making a relatively strong structure. Seven entrances on the surface were inconspicuously located under leaves lying near the periphery; these openings were large, i.e.,

[3]The workers at colony No. 2 were also tending aphids of this species on oaks and aspens. In addition, they were tending coccids (*Kermes* sp., det. Harold Morrison) on red oak branches.

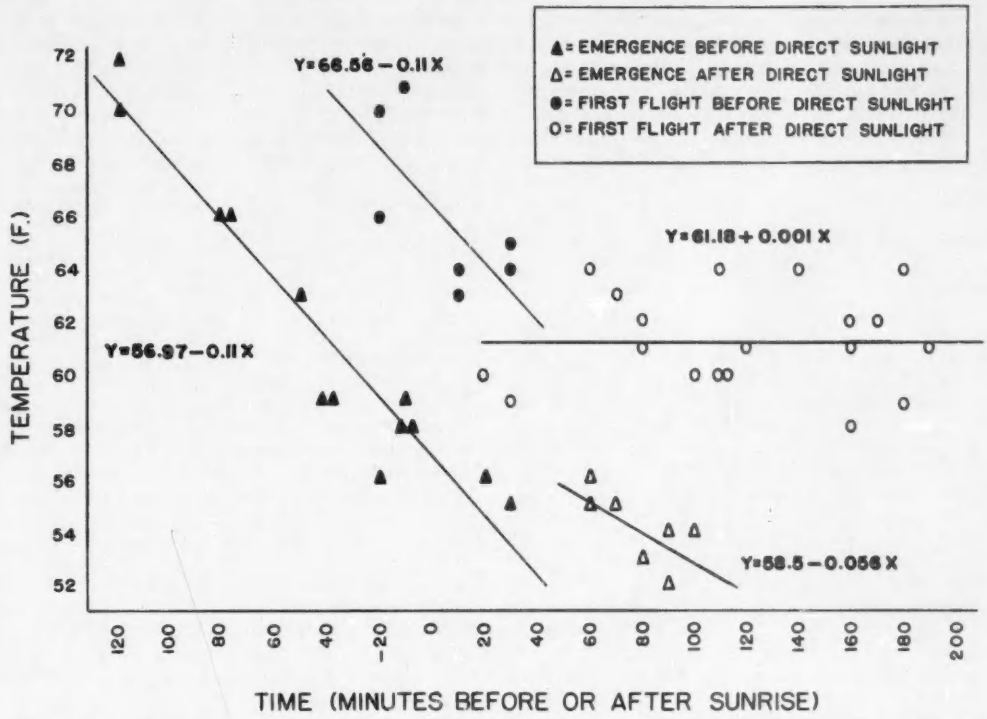


FIG. 2.—Correlation of the time (related to sunrise) of emergence and beginning of flights with the temperature. For both emergence and first flight, the data were divided into two groups, depending upon the presence or absence of direct sunlight on the nest and/or the ants, and separate regression lines were calculated for each group.

from 25 to 35 mm. long and 3 to 7 mm. wide. Two additional openings—3 and 4 mm. in diameter—were present beside plant stems which passed through the roof. There was no evident modification of the nest surface prior to or during the flight season. I opened the nest only partially so as not to disrupt the colony too much. The sandy soil had been excavated to a depth of approximately 45 cm., forming one large chamber. There was no evidence of this soil near the nest, so that it probably was scattered at random at some distance from the nest. Underground stems and roots penetrated this chamber and were used by the ants in making several shelves or partitions of fragments of stems and leaves. These projections served as supports for the masses of workers and brood of the colony.

CLIMATIC CONDITIONS

The climatic conditions during which flight activities occurred have been summarized in table 1. All flight activities took place in early morning. Flights took place daily except on rainy mornings. The frequency of flight occurrence in relation to the time before or after sunrise is presented in figure 1. The influence of temperature[4] upon the time of emergence and of the beginning of flights is shown in figure 2. At air temperatures below 55° F. no alates emerged from the nest unless it was receiving direct sunlight, and alates emerging under these conditions rarely flew until the temperature reached 58° to 64° F., perhaps several hours later. At temperatures between 55° and 62° F. alates emerged but did not fly before the first rays of sunlight covered them. At temperatures of 63° F. or higher the alates emerged and began their flights before the sunlight reached the nest. The frequency of flight occurrence at various early morning temperatures is presented in figure 3.

The relative humidity about 10 cm. above the nest surface varied moderately during flights (table 1), but seemed not to influence the occur-

[4]The temperatures on which the following discussion and the text figures are based are air temperatures recorded about 10 cm. above the nest. The alates probably were stimulated to fly by air temperatures. For emergence, however, the alates most likely responded to nest temperatures, which in early morning averaged 10 to 12 degrees (F.) higher than air temperatures. Unfortunately, not enough records of nest temperatures at the time of emergence were obtained for use here.

Table 1.—Summary of climatic conditions during which flight activities of *Dolichoderus taschenbergi* took place.

	Time (A.M.)	Temperature (°F.)	Relative humidity, percent	Sky	Light (C./sq. ft.)	Wind
Emergence of alates	3:20–6:50	52–72	84–99	clear to cloudy	0–100	calm to moderate
Beginning of flights	4:45–8:20	58–71	86–99	clear to cloudy	10–400	calm to moderate
End of flights	5:25–9:10	63–72	80–99	clear to cloudy	40–750	calm to moderate

rence of flights or their size or duration. The humidity was always high in early morning; the lowest readings were those at the end of the flight period on late-morning flights (8:00–9:10). The presence or absence of cloud cover had little direct effect on the flights. Sky conditions indirectly affected flights on cold mornings; then, flights occurred much earlier under clear skies, evidently because the direct sunlight warmed the alates. Slight to heavy ground fogs sometimes occurred in the early mornings but did not interfere with the flights.

Light intensity may have influenced the initiation of flights. On warm mornings alates started to emerge from the nest as early as 118 minutes before sunrise, at which time no reflected light was registered on the meter. The alates then remained on the vegetation until nearly the time of sunrise before flying, even though the temperature, relative humidity, and wind conditions remained approximately constant. Slight to moderate winds seemed not to affect flights, but short, strong gusts brought about a temporary cessation of activities. A few seconds after the wind died down, activities resumed, often with increased vigor.

FLIGHTS

Preflight behavior.—At the beginning of each flight day the alates, usually both sexes at the same time, gathered at the openings in the early morning hours. Generally, they remained there only briefly and then began to emerge singly. Emergence of the alates that were to take part in a flight usually took place within a period of 15 to 30 minutes. On warm mornings the alates slowly moved out onto the surface and up the stems of adjacent plants. On cool mornings they formed clusters on the surface near the openings. The ants milled about in the clusters, but each cluster maintained approximately the same position. Then, as the temperature increased, or as direct sunlight struck the nest, the alates began, a few at a time, to crawl slowly up the stems and move to high projections on the stems and leaves. The alates usually remained on the vegetation for an hour or more, some moving about frequently, others remaining quiet, apparently awaiting suitable flight conditions. Usually, as flight time neared, each alate moved to the end of a stem or leaf and, holding on to the projection with all legs, fluttered its wings. Often the alate next moved to a different site and fluttered its wings again. Fluttering usually began 10 to 30 minutes prior to the first flight. The alates fluttered their wings for 1 to 8 seconds at a time, with a mean of approximately 3 seconds. Many alates were observed moving the gaster up and down during fluttering, possibly for balance. Workers seemed to have little influence on preflight behavior; they always preceded the alates in emerging from the nest and in moving onto the nearby vegetation. Their activity, which was most noticeable on cold mornings, seemed to be a type of guarding. On warm mornings the workers, although present, paid little attention to the alates.

Flight behavior.—Having selected a prominence on the vegetation and holding on to it, usually with all legs but occasionally with only the middle and hind pairs, the alate fluttered its wings. It then became airborne by releasing its hold on the vegetation while fluttering. Traveling into the air at angles varying between 30° to 80° from the horizontal, but usually from 30° to 60°, the alates moved mostly in a southeasterly direction over the open field and out of sight. Mating did not occur on the surface, and there was no evidence that it took place within the nest. Presumably, the alates pair and copulate during or after the flights.

Once a flight commenced, it continued uninterrupted until all that day's alates had flown. However, the number of alates taking flight varied considerably during the flight period. On an average flight day very few alates flew during the first 15 minutes. The number increased gradually, with most of the alates taking flight within 10 to 30 minutes near the middle of the flight period. The number taking flight then gradually diminished; only about a dozen alates remained during the last 5 to 10 minutes. Often at the end of a flight there were still a few alates on the vegetation, but these were almost always cripples—alates with deformed wings—which were unable to fly. Males and females began to

fly at approximately the same time, but the former usually were the first to fly. Males predominated during most flights, but near the end of the flight season females occurred in about equal numbers with the males. I estimated that about 80 percent of the alates that flew during the entire season were males. The speed of flight varied from 2 to 5 feet per second, without any significant difference between males and females.

Most flights ended when all the alates that had emerged from the nest had flown. On a few days (especially on cool mornings, when the flights started late and lasted until about 9:00) some workers moved over the stems and leaves, near the end of the flight period, stimulating the alates to fly or to return to the nest. The shortest complete flight lasted 20 minutes; the longest flight lasted 2 hours. The mean flight duration was 66 minutes.

The flights were mostly of moderate size, the mean number of alates in 24 flights being 369. The smallest flights—about 50 alates—occurred during the last few flight days. The largest flight, which comprised about 2,500 alates, took place early in the flight season after rain had prevented a flight on the previous day. Most flights consisted of 300 to 400 alates. Probably 12,000 to 15,000 alates flew from this colony during the flight season.

Alates perambulated over the surface of the nest each day during the flight season. Males and females, usually 10 to 30 at a time, came out of the nest near the end of the morning flight and moved slowly and randomly over the nest surface. This parading was observed at various hours of the day and night, but most frequently in late morning and midafternoon. On warm (70°+F.) nights the alates were observed perambulating on the nest after midnight. Parades of *D. taschenbergi* alates have previously been observed by Logier (1923) in Ontario.

COMPARISON WITH *Dolichoderus mariae* FLIGHT ACTIVITIES

The flight activities of all of the North American species of *Dolichoderus* except *D. taschenbergi* have already been compared (Kannowski, op. cit.). Thus, the activities of *D. taschenbergi* will be compared here only with those of *D. mariae* (Talbot, op. cit., and Kannowski, op. cit.), which is its closest congener in North America.

The flight seasons of these two species are distinct. The flight season of *D. taschenbergi* extends from mid-June to the end of July; that of *D. mariae* occurs from early August to mid-September. This distinctness of the flight seasons is evidently due to differences in time of the year when the colonies become active and when the first eggs are laid. Eggs which are laid by a *D. taschenbergi* female in April begin to develop into workers, alate females, and males in early June. On the other hand eggs of *D. mariae* are not laid until late May and June; they develop into alates and workers in August and early September. The flight periods (the time of day of flights) of the two species are similar (5:28 to 10:45 a.m. for *D. mariae;* 4:45 to 9:10 a.m. for *D. taschenbergi*). Both species have mean flight durations of approximately 1 hour.

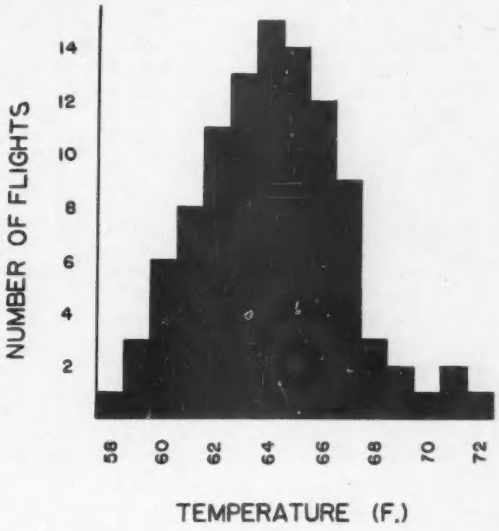


FIG. 3.—Frequency histogram of the occurrence of flights at the various early-morning temperatures prevailing when such flights took place.

These two species seem to be adapted to approximately the same temperatures for flights. Flights from a bog nest of *D. mariae* took place at 56° F., but only when the nest and the alates were warmed by direct sunlight. The hillside nest of this species observed by Talbot was hidden from direct sunlight until late morning; here, flights occurred only at temperatures of 63° F. or higher. Alates of *D. taschenbergi* flew at 58° F. when in direct sunlight and at a minimum of 63° F. prior to sunlight reaching the nest. Flights of both species take place at hours when the relative humidity usually is high; no direct effect of low relative humidity was noted on any flights. Neither species had flights on rainy mornings or during strong winds.

The alates and workers of both species are similar in their preflight behavior. After emergence from the nest the alates climb up the adjacent vegetation, evidently seeking prominences from which to fly. The speed at which the alates climb up the plants seems related to the environmental conditions, being slower on cold, cloudy mornings. In general there is little influence by the workers during emergence and preflight activities, especially for *D. taschenbergi*.

However, this activity on the part of the workers is likely correlated with temperature and thus would be more evident during *D. mariae* flights because of the generally cooler temperatures at the time of the year when flights of this species occur. Both species have similar behavior during the selection of flight prominences, which are almost always stems and leaves of adjacent upright vegetation. Fluttering prior to flight is common to the alates of both species, and they also show similar angles of flight and flight speed. The direction of flight is somewhat variable, but the alates seldom move toward the sun; most fly to the right or left of the sun, but rarely away from it. Undoubtedly, local vegetation patterns affect the flight direction because of shading.

The total flight populations of individual colonies of the two species are similar. Estimates for *D. mariae* include 8–10,000 (Kannowski, op. cit.) and 15,000 (Talbot, op. cit.), while 12–15,000 have been estimated to have flown from the *D. taschenbergi* colony. The number of alates flying varied considerably from day to day. While the bog nest of *D. mariae* rather consistently had flights of 300–800 alates per day (Kannowski, op. cit.), more than two-thirds of the total estimated number of *D. mariae* alates flew from the hillside nest on 4 days (Talbot, op. cit., p. 136). The size of daily flights of *D. taschenbergi* most closely resembles those of the bog nest of *D. mariae;* however, one extremely large flight (2,500 alates) was noted.

Usually, the flights of both *D. mariae* and *D. taschenbergi* ended when all the alates capable of flight had flown. Often the flights of *D. mariae* were terminated by workers forcing the alates to return to the nest, and this was observed several times at the *D. taschenbergi* nest. Near the end of the flights alates of both species begin to perambulate on the tops of the nests. These parades have been observed during daylight hours at nests of both species, but only at the *D. taschenbergi* nests at night.

REFERENCES CITED

Brown, W. L., Jr. 1950. Morphological, taxonomic, and other notes on ants. Wasmann Jour. Biol. 8(2): 241–50.

Creighton, W. S. 1950. The ants of North America. Bull. Mus. Comp. Zool. 104: 1–585.

Kannowski, P. B. 1959. The flight activities and colony-founding behavior of bog ants in southeastern Michigan. Insectes Sociaux 6(2): 115–63.

Logier, S. 1923. An interesting ant from Muskoka. Canadian Ent. 55(11): 247–9.

Talbot, Mary. 1956. Flight activities of the ant *Dolichoderus* (*Hypoclinea*) *mariae* Forel. Psyche 63(4): 134–9.

Wheeler, W. M. 1905. The North American ants of the genus *Dolichoderus*. Bull. Amer. Mus. Nat. Hist. 21: 305–19.

STUDIES OF THE VERTICAL DISTRIBUTION OF THE CLOVER ROOT BORER IN ROOTS OF RED CLOVER IN RELATION TO PROGRESSION OF THE SEASON[1]

C. S. KOEHLER AND GEORGE G. GYRISCO
Cornell University, Ithaca, N. Y.

ABSTRACT

Red clover roots were sampled periodically from a first-harvest-year field, cut into ½-inch segments starting at the top of each root, and examined for numbers of the clover root borer, *Hylastinus obscurus* (Marsh.) (Coleoptera: Scolytidae). For the period June 12 to October 12, 1957, the seasonal average depths were: larvae, 0.76 inch; pupae, 0.84 inch; and adults, taken after the first callow individual appeared, 0.82 inch. The pooled average depth of these stages increased in a linear manner as the season progressed. Using head-capsule width as a criterion of size, the depth of larvae collected on August 22 was directly proportional to their size. Temperature appeared not to be a controlling factor for the depth at which the combined stages were found. In the absence of a temperature effect, maturity seemed to be the factor that had the greatest influence on the depth at which larvae were located.

Unlike other members of the family Scolytidae, the clover root borer, *Hylastinus obscurus* (Marsh.), is associated primarily with red clover, *Trifolium pratense* L. The eggs are deposited during the spring and summer in niches located in the walls of the oviposition gallery, which is formed entirely within the tap root. Upon egg hatch, the larvae excavate sinuous feeding galleries within the root tissue and pupate in enlarged chambers at the terminal ends of the galleries. The new adults continue to feed as long as favorable temperatures persist and normally remain in the roots during the winter. The following spring adult dispersal takes place, when borers leave the roots and migrate to other plants in the same or distant fields.

Since the borer is found in nearly every red clover field in New York, as well as the majority

[1]Accepted for publication April 27, 1959.

of areas in the United States where red clover is an important agricultural crop (Rockwood 1926), intensive studies were initiated on its biology in 1939. The present paper is the result of some of the investigations conducted during 1956 and 1957, and deals with the relation between seasonal progression and the vertical distribution of several stages of the borer in the root.

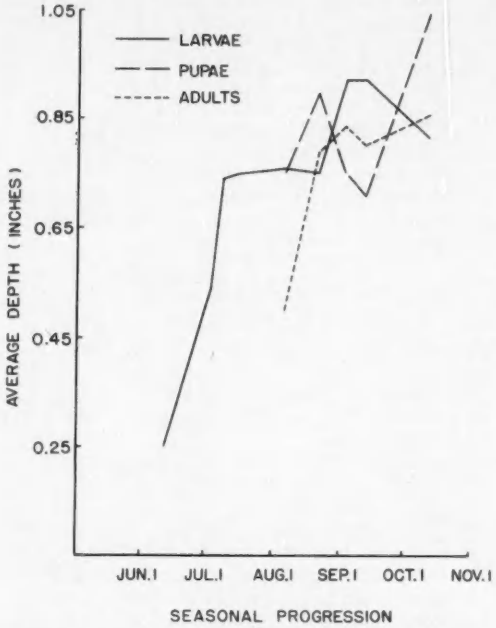


FIG. 1.—Average depths in red clover roots at which different stages of the clover root borer were found on each sampling date in 1957.

METHODS

During the period from April 25 to October 12, 1957, red clover plants were taken at irregular intervals from a first-harvest-year[2] field located in Oswego County, New York. Each root was cut into 0.5-inch segments, starting at the crown, and then dissected under magnification. The numbers of larvae, pupae, and adults found in each segment of root were recorded.

All the larvae collected on August 22, 1957, were held by separate root segment for measurement of the greatest width of the head capsule. These data were used as an index of size, or maturity. The range of measurements encountered was arbitrarily divided into eight equal groupings, and each individual was placed into the appropriate grouping according to its size.

[2]The term "first harvest year" refers to the first calendar year after the year in which the seeding was made.

In conjunction with studies reported elsewhere (Koehler and Gyrisco 1959), a number of plants was taken December 18, 1956, from a different red clover field in the same county. These roots were dissected and examined for borers as described above.

Data treated statistically were analyzed using regression procedures. The 5-percent level was arbitrarily chosen to test significance.

RESULTS AND CONCLUSIONS

The average depths at which larvae, pupae, and adults were located on the nine sampling

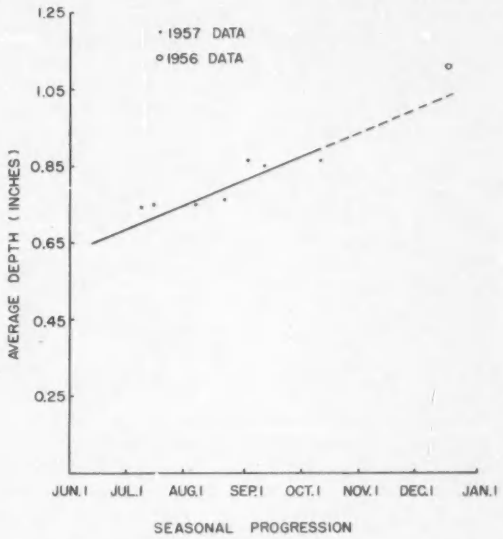


FIG. 2.—Regression of average depth in roots, of clover root borer larvae, pupae, and adults, on seasonal progression.

dates in 1957 are presented in table 1. Larvae, first found on June 12, were located primarily within 1.5 inches of the root tops. The 743 individuals collected were found at an average depth of 0.76 inch below the top of the root. Larvae were still present on October 12, the last date on which roots were sampled in 1957.

Pupae first appeared August 7 and were present on the last sampling date. Most of the pupae were located within the uppermost 1.5 inches of root. The mean seasonal depth of the 67 individuals of this stage taken was 0.84 inch.

Adults of the new generation, that is, those resulting from eggs deposited during the spring of 1957, first appeared in roots examined August 7, although older adults were found both before and after this date. Individuals taken during the sampling period were found mainly in the uppermost 2 inches of root; the mean seasonal depth for the 127 adults taken was 0.82 inch.

Table 1.—Depth at which various stages of the clover root borer were found in first-harvest-year roots in 1957.

Sampling date	Total number		Average depth in inches below the root top			
	Roots examined	Individuals found	Larvae	Pupae	Adults[a]	All stages
June 12	45	1	0.25			0.25
July 4	75	50	0.54			0.54
July 9	75	125	0.74			0.74
July 16	75	143	0.75			0.75
August 7	45	158	0.76	0.75	0.50	0.75
August 22	45	172	0.75	0.89	0.78	0.77
September 3	45	110	0.92	0.75	0.83	0.87
September 12	45	83	0.92	0.71	0.80	0.85
October 12	30	94	0.81	1.04	0.86	0.87

[a]Only adults taken on and after August 7 shown. First callow adult was taken on that date.

Figure 1 suggests that borer depth is related in some way to seasonal progression. If this relation were attributable to soil temperature, it would be expected that depth, after generally increasing during the heat of summer, would decrease again with the advent of cooler fall temperature. However, a multiple regression analysis, weighted to compensate for the unequal numbers of individuals found on each sampling date failed to support the hypothesis of an effect due to temperature. The depth of all borer stages combined increased in a linear manner as the season progressed from June 12 to October 12, 1957, with no significant curvilinear tendency (figure 2).

Table 2.—Depths at which 102 larvae, taken August 22, 1957, were found in first-harvest-year red clover roots.

Range in head capsule width (mm.)	Average group size in mm.	Number of larvae	Average depth in inches below the root top
0.334 to 0.374	0.354	10	0.60
.375 to .415	.395	7	.54
.416 to .456	.436	16	.66
.457 to .497	.477	5	.59
.498 to .538	.518	16	.76
.539 to .579	.559	19	.81
.580 to .620	.600	20	.98
.621 to .662	.641	9	.92

The roots examined in December 1956, contained a total of 120 borers, which were considered to be overwintering individuals. Of these, 80 percent were adults, 18 percent were larvae, and 2 percent were pupae. The overwintering depths of the various stages did not differ appreciably from one another, and the combined average depth for all stages was 1.10 inches below the root crown. Although these data pertain to a different root borer population than those considered earlier, the average depth of these individuals approximates that which is obtained upon extrapolation of the regression line shown in figure 2.

Further information on the vertical distribution of borers in roots was obtained with the use of the 102 larvae collected on August 22, 1957. The overall head-capsule width range extended from 0.334 mm. to 0.662 mm. From other (unpublished) studies it is known that such a range includes individuals of all instars (table 2). A significant linear regression of average larval depth on average head capsule width was found ($r^2 = 0.8733$), with larvae increasing their depth as their size increased. Since all the larvae were collected on a single date, it seems evident that the variations in depth at which they were found cannot be accounted for by variations in temperature. It is believed that in the case of larvae, and perhaps for other stages as well, maturity is the factor that has the greatest influence on depth.

ACKNOWLEDGMENTS

The authors are grateful for the assistance given by H. H. Shorey and George O. Poinar, Jr., who helped in certain phases of this work.

REFERENCES CITED

Koehler, C. S., and **George G. Gyrisco.** 1959. Effect of root size and soil moisture on the number of clover root borers present in red clover roots. Jour. Econ. Ent. 52(4): 658–60.

Rockwood, L. P. 1926. The clover root borer. U. S. Dept. Agric. Dept. Bull. 1426. 48 pages.

THE HYDROGEN-ION CONCENTRATION IN THE ALIMENTARY CANAL OF BEETLES INFESTING STORED GRAIN AND GRAIN PRODUCTS[1]

R. N. SINHA[2]

ABSTRACT

Wheat flour, in separate mixtures with eight different pH indicators, was fed to 10 species of small, stored-grain-infesting beetles. In the 575 individuals dissected, the pH of fore-, mid-, and hindgut, respectively, ranged as follows: *Cryptolestes ferrugineus*, 4.6 to 5.2, 5.2 to 6.0, 4.6 to 5.2; *C. turcicus*, 3.6 to 4.6, 5.2 to 6.8, 4.6 to 5.2; *Oryzaephilus mercator*, 4.6 to 5.2, 5.2 to 6.8, 4.6 to 5.2; *O. surinamensis*, 5.2 to 6.0, 7.2 to 7.6, 3.6 to 5.2; *Rhizopertha dominica*, ca. 6.8, 5.2 to 7.2, 3.6 to 4.6; *Sitophilus granarius*, ca. 5.2, 6.8 to 8.4, 4.6 to 5.2; *Tribolium castaneum*, ca. 5.2, 7.2 to 7.6, 3.6 to 4.6; *T. confusum*, 4.6 to 5.2, 5.2 to 6.8, 3.6 to 4.6; *Trogoderma parabile*, 5.2 to 6.0, 7.2 to 8.0, 3.6 to 4.6; and *T. versicolor*, 5.2 to 6.8, ca. 6.8, 3.6 to 4.6.

The pH of the alimentary canal of adults of various species of Coleoptera has been studied by Swingle (1931), Krüger (1933), Staudenmayer (1940), and Grayson (1958). The present study was undertaken as part of a general project to investigate the morphological and physiological adaptations of the gut in beetles in relation to their specialization for feeding on stored cereals or cereal products. The morphological findings have been published elsewhere (Sinha 1958a, 1958b). The pH of different regions of the alimentary canal of the following 10 species representing six genera of the order Coleoptera has been described in this paper: *Cryptolestes ferrugineus* (Steph.), *C. turcicus* Grouv., *Oryzaephilus mercator* (Fauval), *O. surinamensis* (L.), *Rhizopertha dominica* (L.), *Sitophilus granarius* (L.), *Tribolium castaneum* Herbst, *T. confusum* Duv., *Trogoderma parabile* Beal, and *T. versicolor* (Creutzer).

MATERIALS AND METHODS

All insects used in this study were taken from stock cultures maintained in the laboratory at room temperature and relative humidity, except for *Tribolium castaneum*, *T. confusum*, *Oryzaephilus surinamensis*, and *O. mercator*, which were reared at 30° C. and 70 percent relative humidity. The method used by Waterhouse (1940) and Day and Powning (1949) was found most satisfactory for the determination of pH of the gut contents of these small insects. However, the observed pH values were cross-checked, following a suggestion of Waterhouse (in litt.), by indicator papers and by mixing particles of indicators directly with the contents of the gut. To evaluate the pH of the intrinsic secretions of the gut cellulose powder, an indigestible food was mixed with the pH indicators and fed to *C. ferrugineus* and *Tribolium confusum* (Waterhouse in litt.). Mature adults were starved for 1 to 7 days, depending upon the ability of each species to endure starvation. They were then allowed to feed on a mixture of wheat flour (60 mesh) and a pH indicator in powdered form for periods of 2 minutes to 4 hours. Eight pH indicators,[3] Bromo-phenol blue (2.8–4.6), Bromo-cresol green (3.6–5.2), Bromo-cresol purple (5.2–6.8), Bromo-phenol red (5.2–7.0), Thymol blue (1.2–2.8, 8.0–9.6), Bromo-thymol blue (6.0–7.6), Phenol red (6.8–8.4), and Cresol red (7.2–8.8) were used. After the insects had fed, they were dissected under a binocular microscope and the color of the foregut, anterior midgut, posterior midgut, ileum, and rectum was immediately recorded. Five hundred and seventy-five dissections were made for the whole study and at least five insects were used for each of the eight indicators.

RESULTS

The pH of different parts of the alimentary canal of 10 species of insects infesting stored products has been summarized in table 1. The pH of the food was approximately 6.0.

The pH of the foregut of all the species was acid and ranged from 3.6 to 6.8. The anterior three-quarters of the midgut was acid in all the species except *O. surinamensis*, *Tribolium castaneum* and *Trogoderma parabile*, in which it was alkaline throughout the whole midgut. In *R. dominica* the pH changed from acid in the anterior midgut to neutral in the posterior midgut, while in *Trogoderma versicolor* it remained the same in both portions of the midgut. In *S. granarius*, the pH of the posterior midgut was the highest, being about 8.4. In *Cryptolestes ferrugineus*, *C. turcicus*, *O. mercator*, and *Trobilium confusum*, the posterior midgut was slightly more acid than the anterior. The hindgut, in general, ranged in pH from 3.6 to 6.8; the rectum usually had a lower pH than that of the ileum.

DISCUSSION

Swingle (1931), Krüger (1933), and Grayson (1958) found that the pH of the foregut of all the 30 species of adult Coleoptera examined by

[1]Contribution No. 22 from Research Station, Research Branch, Canada Agriculture, Winnipeg, Manitoba. Accepted for publication April 20, 1959.

[2]Entomologist, Entomology Section.

[3]Indicators were purchased from British Drug Houses (Canada), Ltd., Toronto, Canada.

Table 1.—The pH of various regions of the alimentary canal of 10 species of stored-grain beetles.

Insect	Foregut	Midgut		Hindgut	
		Anterior[a]	Posterior[b]	Ileum	Rectum
Cryptolestes ferrugineus	4.6–5.2	5.2–6.0	ca. 5.2	4.6–5.2	4.6–5.2
C. turcicus	3.6–4.6	5.2–6.8	5.2–6.0	4.6–5.2	4.6–5.2
Oryzaephilus mercator	4.6–5.2	6.0–6.8	5.2–6.0	5.2–6.8	4.6–5.2
O. surinamensis	5.2–6.0	7.2–7.6	7.2–7.6	4.6–5.2	3.6–4.6
Rhizopertha dominica	ca. 6.8	5.2–6.8	7.0–7.2	3.6–4.6	ca. 3.6
Sitophilus granarius	ca. 5.2	6.8–7.0	ca. 8.4	ca. 5.2	4.6–5.2
Tribolium castaneum	ca. 5.2	7.2–7.6	7.2–7.6	3.6–4.6	3.6–4.6
T. confusum	4.6–5.2	ca. 6.8	ca. 5.2	3.6–4.6	ca. 3.6
Trogoderma parabile	5.2–6.0	7.2–8.0	7.2–8.0	3.6–4.6	3.6–4.6
T. versicolor	5.2–6.8	ca. 6.8	ca. 6.8	3.6–4.6	3.6–4.6

[a]Anterior three-quarters.
[b]Posterior one-quarter.

them ranged from 5.91 to 8.30, while my observations indicated that the pH is less than 6.8 in all 10 species. As suggested by Day and Powning (1949) in their study on *Blattella*, the preponderance of carbohydrate in wheat flour ingested by insects infesting stored products may be responsible for the low pH in the foregut of these insects. However, the pH values of the midgut of the insects studied by me, although feeding on the same type of food, vary in a way similar to those of beetles having different diets. The pH values of the midgut of all the stored grain beetles except *S. granarius* confirm the conclusions drawn by Grayson (1958) that coleopterous insects feeding on grain products have an alkaline to acid reaction in the midgut. It may be interesting to note that the pH of the midgut differs even in the closely related species of the genera *Oryzaephilus*, *Tribolium*, and *Trogoderma*, viz., in *O. mercator*, *Tribolium confusum*, and *Trogoderma versicolor* it is acid, while in *O. surinamensis*, *Tribolium castaneum*, and *Trogoderma parabile* it is alkaline. The differences in the pH of the midgut of closely related species may possibly be correlated with the food habits of their ancestors. Similarly, the presence of a proventricular valve in the alimentary canal of *O. surinamensis* and its absence in *O. mercator* may also be explained on a similar postulate (Sinha 1958a). Krishna (1955) first recorded the pH of the hindgut of an insect infesting stored grain (*Trogoderma*[4] larva) to be strongly acid (pH 4.6 to 4.8). The low pH values of the beetles infesting stored grain presented in this paper, including those of *Trogoderma parabile*, agree with the findings of Krishna.

The pH of the hindgut, especially the rectum of stored grain beetles, is more acid, 3.6 to 5.2, than that of any other species of adult Coleoptera that have been investigated so far. The test for bacteria, using Burkholder and Hagborg's method (Hagborg 1957), gave negative results (except for a few rod-shaped bacteria in *Tribolium confusum*). No difference could be detected in the pH patterns in *C. ferrugineus* and *Tribolium confusum* when fed on cellulose. This showed that these low pH values are characteristic of the hindgut alone and are independent of the carbohydrate diet. Day and Powning (1949) also observed that the carbohydrate diet does not reduce the pH of the hindgut in *Blattella*. At this stage, therefore, no definite explanation can be offered for the low pH in the hindgut of these insects. Although no histological difference was observed between the anterior and posterior portions of the midgut of certain stored grain beetles (Sinha 1958a, 1958c), distinct physiological zonation was indicated in some species, e.g., *Tribolium confusum*. Perhaps this signifies that different enzymes are secreted from different parts of the midgut.

[4]Krishna (1955) did not mention the specific name of the *Trogoderma*, but referred to it as one of the most important pests of stored grain in India. Probably it was the Khapra beetle, *T. granarium* Everts.

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. D. F. Waterhouse, Division of Entomology, Commonwealth Scientific & Industrial Research Organization, Canberra, Australia, and Dr. P. D. Gupta, Department of Entomology, University of Manitoba, Winnipeg, for their critical review of the manuscript.

REFERENCES CITED

Day, M. F., and **R. F. Powning.** 1949. A study of the processes of digestion in certain insects. Australian Jour. Sci. Res. (B) 2(2): 175–215.

Grayson, J. M. 1958. Digestive tract pH of six species of Coleoptera. Ann. Ent. Soc. America 51(4): 403–05.

Hagborg, W. A. F. 1957. Maintenance of contaminant-free stain preparations for the detection of bacteria in plant tissues. Phytopath. 47(10): 628.

Krishna, S. S. 1955. Physiology of digestion in *Trogoderma* larva. Jour. Zool. Soc. India 7(2): 170–6.
Krüger, P. 1933. Vergleichender Fermentstoffwechsel der niederen Tiere. Ergebn. Physiol. 35: 538–72.
Sinha, R. N. 1958a. Similarities in the histology of the gut of some species of *Tribolium* Macleay (Coleoptera, Tenebrionidae) and *Oryzaephilus* Ganglbauer (Col., Cucujidae). Canadian Ent. 90(3): 129–45.
1958b. Movement of food in the gut of some adult stored grain beetles. Canadian Ent. 90(4): 202–12.
1958c. The alimentary canal of the adult of *Tribolium castaneum* Herbst (Coleoptera, Tenebrionidae). Jour. Kansas Ent. Soc. 31(2): 118–25.
Staudenmayer, T. 1940. Die Wasserstoffionenkonzentration der Insekten. Anz. Schadl. 16: 114–9.
Swingle, M. C. 1931. Hydrogen-ion concentration within the digestive tract of certain insects. Ann. Ent. Soc. America 24(3): 489–95.
Waterhouse, D. F. 1949. The hydrogen-ion concentration in the alimentary canal of larva and adult Lepidoptera. Australian Jour. Sci. Res. (B) 2(4): 428–37.

SCIENTIFIC NOTES

Haplothrips clarisetis in Southern California (Thysanoptera: Phlaeothripidae)[1]

W. H. Ewart and O. L. Brawner
University of California Citrus Experiment Station, Riverside

A species of Phlaeothripidae tentatively identified as *Haplothrips clarisetis* Priesner, has recently been collected in southern California. Previous distribution records for this species include Africa, Palestine, and Jordan (Priesner 1930, 1936, 1937, 1950; Jacot-Guillarmod 1937; Faure 1955).

The first California specimens were taken from flowers of the common dandelion *Taraxacum vulgare* (Lam.) Shrank, on March 17, 1956, in the city of Riverside. Since then, adult females have been found throughout the year in a wide variety of flowers. Greatest numbers occur, however, on Russian thistle, *Salsola kali* var. *tenuifolia* Mey., in December and January when hundreds of larvae and adult females can be shaken from a single plant. Larvae have also been collected from iceplant, *Mesembryanthemum* spp. Apparently *Haplothrips clarisetis* is well established in southern California, since it has been found in Riverside, San Bernardino, Imperial, Ventura, and Los Angeles Counties. It has also recently been reported from New Mexico (Anonymous 1959, Watts 1959), indicating it may be widespread in southwestern United States.

Because of the occurrence of large numbers of specimens, it was assumed at first that a species of *Haplothrips*, well-known in California, was being collected. When its description was found not to agree with descriptions of the California species listed by Cott (1956), however, specimens were sent to various authorities for examination. Stanley F. Bailey, University of California, Davis, was unable to find it represented in any collection of California *Haplothrips* known to him. Miss Kellie O'Neill, of the U. S. Department of Agriculture, Washington, D. C., identified it as *H. clarisetis* of very near. J. C. Faure, of Pretoria, Union of South Africa, agreed with Miss O'Neill, but indicated that a more conclusive identification would require a comparison of males from California and Africa. So far this has not been possible, however, as males have not been found in California.

Faure (1955) published complete descriptions of adults of both sexes of *Haplothrips clarisetis*. In the key to adults of the California species of *Haplothrips* prepared by Cott (1956), *H. clarisetis* goes to couplet 4 with *H. maliflоris* Hood. *H. clarisetis*, however, has expanded tips on most of the major dorsal body bristles and a rounded mouthcone, while *H. maliflоris* has acute body bristles and a pointed mouthcone.

The only description of the larvae of *H. clarisetis* found in the literature is a notation by Priesner (1937) that the head and prothorax are red in color and that the b. 3 bristles on the posterior margin of abdominal segment IX are pointed. Living larvae collected in California are strikingly colored with brown, red, and yellow. The antennae are uniformly dark brown, except joint 2, which is brown in the basal three fourths and abruptly yellow in the distal one fourth except for a brown ring at the tip. Other brown areas include the head, legs, pronotal plates, abdominal segments IX and X, and small areas at the bases of the dorsal bristles of the thorax and abdomen. In the second instar, additional brown areas include the lateral plates of abdominal segment VIII and three pairs of small irregular spots on the meso- and metanotum. Internally, a red pigment occurs in the head, prothorax, and the three terminal abdominal segments, while a yellow pigment occurs in the remaining portions of the thorax and abdomen. Both the red and the yellow pigments tend to fade and to disappear in a few weeks in alcohol-preserved specimens. Almost all the major dorsal bristles on the larvae have expanded tips. Exceptions are a pair of short pointed bristles on the pronotum (one on the inner anterior angle of each pronotal plate) and a pair of long, blunt bristles on the median posterior margin of abdominal segment IX.

Living pupae reared in the greenhouse on Russian thistle are predominantly red in color with the middle portion of the body shading to yellowish-red. The antennae and wing pads are almost colorless.

The large numbers of *Haplothrips clarisetis* collected in southern California since 1956 indicate it was recently introduced. Although it is not known as yet to cause damage to any commercial crop in this state, it must be regarded as a potentially serious pest in view of the recent report (Anonymous 1959, Watts 1959) of damage to lettuce in New Mexico.

REFERENCES CITED

Anonymous. 1959. U. S. Dept. Agric. Coop. Insect Report 9(13): 215.
Cott, H. E. 1956. Systematics of the suborder Tubulifera (Thysanoptera) in California. Univ. California Publ. Ent. 13: 1–210.
Faure, J. C. 1955. South African Thysanoptera 4. Jour. Ent. Soc. Southern Africa 18(2): 208–34.
Jacot-Guillarmod, C. F. 1937. Ten new species of Thysanoptera and a catalogue of the known South African forms. Univ. Pretoria Publ., Ser. 2, Nat. Sci. No. 3: 1–62.
Priesner, H. 1930. A review of the African *Haplothrips* species. Bull. Soc. Roy. Ent. d'Egypte 14: 230–7.
1936. Studies on the genus *Haplothrips* Serv. Ibid. 20: 61–75.
1937. Contributions towards a knowledge of the Thysanoptera of Egypt, XI. Ibid. 21: 208–22.
1950. Further studies in *Haplothrips* and allied genera (Thysanoptera). Bull. Soc. Fouad 1er Ent. 34: 69–120.
Watts, J. G. 1959. Tubulifera thrips damage to lettuce. Jour. Econ. Ent. 52(4): 786.

[1]Paper No. 1152, University of California Citrus Experiment Station, Riverside, California. Accepted for publication April 27, 1959.

Strength-Weight Relationships in a Laboratory Population of Tenebrio molitor Adults[1]

BARTLEY C. BLOCK[2]
Department of Biology, Northwestern University, Evanston, Illinois

The literature on insect strength is not extensive, but there is a wide diversity of approaches to the problem and opinions expressed. Plateau (1865, 1866) demonstrated that smaller species have a relatively greater strength than heavier groups. Such insects are thus able to push, pull, lift, or fly with weights much heavier than their own body masses.

Miall and Denny (1886) argued that comparisons of strength and weight between different species contribute little to an understanding of such relationships, and used the mass-surface law of Spencer (1873) to support their thesis. This principle, applicable to biological systems, states that a mass increases by its cube as the surface area is squared. Smaller insects should therefore be favored in measurements of strength.

Hiestand (1929) pointed out an inverse correlation of relative strength and weight in the family Carabidae. Twenty-five genera were studied but only one individual served as representative of each group. The object of the following study was to determine whether the inverse strength-weight relationship exists within a single species.

MATERIALS AND METHODS

Tenebrio molitor Linnaeus was used since it was easy to rear in the laboratory, convenient to handle, of suitable size and weight, and made no attempt to fly. Cultures were kept in 2-gallon, covered crocks, half-filled with bran flakes and small bits of bread and apple.

The apparatus used for measurements of strength consisted of a specially constructed 5-gram dynamometer accurate to 1/100 gram. A trough, which served as a guide to the insects' course during trials, was positioned beneath the dynamometer and lined on the interior with felt to enable the insects to secure maximum traction.

After selection of an adult from a culture crock, a piece of thread was secured to the thorax and elytra by an adhesive. Beeswax was pressed to the other end of the thread and attached to the dynamometer.

A trial began when the insect was positioned at the top of the trough, facing downward and under the influence of a slight backward force. Preliminary experiments showed that insects generally counteracted such forces by pulling in the opposite direction. The beetle descended the trough and was stimulated with a fine brush if it stopped, although balking rarely occurred. When the insect was no longer able to exert itself against the tension of the dynamometer spring, a reading of its maximum strength was recorded. The weight of each individual was determined with an analytical balance after the completion of a trial.

RESULTS

Table 1 presents the strength-weight relationship for 148 beetles. In general, the heaviest insects also pulled the most weight and there was an inverse correlation of relative strength (strength/weight index) and weight. The relationship is only approximate, because of the relatively large variability within each division.

The 0.06-, 0.16-, 0.19-, and 0.22-gram weight divisions, not shown in table 1, each had one representative, pulling 1.33, 3.07, 4.08, and 4.49 grams, respectively. The order of magnitude of their strengths fits reasonably with the data of groups having more than one representative.

DISCUSSION

The inverse relationship between strength and weight found in this study within a single species agrees with the findings of Hiestand on many genera in one family and supports the mass-surface principle. The enormous relative strength of insects when compared to other animals, which follows from physical considerations, has been attributed to the hardness of the exoskeleton (Hiestand 1928, Hinds 1901), properties of invertebrate striated muscle (Hiestand 1928), multiple attachment points internally, giving better leverage (Hutchins 1957), and large number of muscles. All these factors have an influence on the maximum strength of insects, depending upon physiological conditions, stage of life cycle, and age.

For example, Hinds (1901) suggested that the strength of insects under natural conditions is greater than under artificial conditions. Since only magnitudes of forces possibly change, quantitative differences in natural and artificial surroundings were not considered in the present study.

Table 1.—Strength-weight relationships of 148 *Tenebrio molitor* adults of varying ages.

No. of Insects	Weight (gm.)	Strength/ weight index	Strength (gm.)	S.E.
4	0.07	33.00	2.31	± 0.25
11	0.08	32.13	2.57	± 0.15
20	0.09	29.33	2.64	± 0.09
19	0.10	27.50	2.75	± 0.11
40	0.11	27.36	3.01	± 0.11
34	0.12	27.17	3.02	± 0.12
12	0.13	26.08	3.39	± 0.17
5	0.14	21.93	3.07	± 0.22
3	0.15	22.20	3.33	± 0.06

Hinds also pointed out that *Passalus cornutus* adults lost almost 3 percent of their body weight during tests, while controls lost only about 0.6 percent. This weight loss is important when relative indices are compared. The average weights of *P. cornutus* and *T. molitor* were approximately 1.04 and 0.11 gram, respectively. On a proportionality basis, *Tenebrio* would become lighter by about 0.003 gram during a trial, which is small when compared to its total body weight.

REFERENCES CITED

Hiestand, W. A. 1928. A correlation of strength and weight in insects. Ann. Ent. Soc. America 21(4): 601–6.

Hinds, W. E. 1901. Strength of *Passalus cornutus* Fab. Ent. News 12: 257–63.

Hutchins, R. E. 1957. How strong are insects? Nat. Hist. 66(2): 88–92.

Miall, L. C., and **A. Denny.** 1886. The structure and life history of the cockroach (*Periplaneta orientalis*). An introduction to the study of insects. London. (pp. 78–84.)

Plateau, F. 1865. Sur la force musculaire des insectes. Bull. Acad. Roy. Beligique (2) 20: 732–7.

1866. Sur la force musculaire des insectes. Ibid. (2) 22: 283–308.

Spencer, H. 1873. Principles of Biology. Part 2, Chap. 1.

[1]Accepted for publication December 26, 1958.

[2]Present address: Entomology Research Division, Agric. Res. Serv., U.S.D.A. The author is indebted to Professor Orlando Park, under whose direction this investigation was conducted.

Malathion Metabolism in Larvae of Resistant Mosquito Strains[1]

LAWRENCE L. LEWALLEN AND LOREN M. NICHOLSON[2]
California State Department of Public Health, Bureau of Vector Control, Fresno, California

The conversion of the insecticide malathion (0,0-dimethyl S-(1,2-dicarboethoxy) ethyl phosphorodithioate) in vivo to its more toxic oxygen analog, malaoxon (0,0-dimethyl S-(1,2-dicarboethoxy) ethyl phosphorothiolate), has been demonstrated in insects and vertebrates (March et al. 1956; O'Brien 1957). In view of these findings it seemed worthwhile to determine whether or not malathion-resistant *Culex tarsalis* Coquillett larvae from Fresno County (Gjullin and Isaak 1957) converted malathion to its oxygen analog. Paper chromatography was used for this purpose.

MATERIALS AND METHODS

Chromatography of pure compounds.—Paper chromatography employing the reversed phase system as described by March et al. (1954) was employed in this study. Tapered Whatman No. 1 filter paper strips were dipped in 1.0 percent Dow Corning 550 fluid in petroleum ether and allowed to dry on paper toweling. Malathion or malaoxon was applied near the bottom of the strip with a ¼-cc. tuberculin syringe fitted with a 27-gauge needle. The plunger was driven by a modified micrometer. One lambda of 1.0 percent wt./vol. solution (10 gammas) in acetone was applied. The papers were developed by ascending flow with a mixture of 10 parts of n-butanol, 10 parts of water and 1 part of propionic acid. The bottom layer of this mixture was pipetted off and used. After 2 to 3 hours the papers were removed from the test tube and allowed to dry at room temperature after the solvent front was marked. Developed papers were sprayed with a 0.5 percent solution of 2,6 dibromo N-chloro-*p*-quinonimine in cyclo-hexane (Menn et al. 1957). After drying at room temperature, the papers were warmed on a hot plate at approximately 110° C. to develop the color. Chromatograms of each compound were prepared in triplicate. The average Rf values for malathion and malaoxon were 0.07 and 0.90 and their respective colors were pink and brownish-yellow.

Chromatography of Treated Mosquito Larvae.—Fourth-instar larvae of the malathion-resistant strain of *C. tarsalis* were compared with larvae of a susceptible laboratory strain. At the time the comparisons were made the resistant strain was 37 times more resistant to malathion than the susceptible strain based on LC_{90} determinations.

One hundred larvae were placed in a 250-ml. beaker, containing 100 ml. of distilled water. One ml. of a 1.0 percent wt./vol. acetone solution of malathion was added to the water. The treated larvae were held at 70° F. for 30 minutes, after which they were removed by filtration through cheese cloth. While on the cheese cloth, the larvae were thoroughly washed with chloroform. Washed larvae were placed in a test tube tissue grinder and homogenized in 1 ml. of distilled water. The homogenate was centrifuged at approximately 1,000 times gravity for 5 minutes and the resulting supernatant liquid was strained through a double layer of cheese cloth into a small beaker. The extract was then evaporated by an air stream to approximately 0.25 ml.

Larval extracts were applied to silicone papers in the manner described for malathion and malaoxon, except that the extracts were applied to the same area three times and allowed to dry at room temperature between each application. The papers were developed, sprayed with color reagent, and heated in the manner previously described.

DISCUSSION OF RESULTS

Unchanged malathion was not detected in the larval extracts of either strain, but a compound corresponding to the Rf value and color of malaoxon was present in chromatograms of both strains. This appears to indicate that the resistant strain of *C. tarsalis* converts malathion to malaoxon as does the susceptible strain. It does not provide an explanation for this resistance. The study was, however, merely qualitative and does not indicate rates of conversion or quantities of insecticide transformed.

Further studies on the mechanism of malathion resistance are in progress in which the possible degradation of malaoxon in resistant strains will be studied.

REFERENCES CITED

Gjullin, C. M., and **L. W. Isaak.** 1957. Present status of mosquito resistance to insecticides in the San Joaquin Valley in California. Mosquito News 17: 67–70.

March, R. B., R. L. Metcalf, and **T. R. Fukuto.** 1954. Paper chromatography of the systemic insecticides, demeton and schradan. Jour. Agric. Food Chem. 2: 732–35.

March, R. B., T. R. Fukuto, R. L. Metcalf, and **M. G. Maxon.** 1956. Fate of P^{32}-labelled malathion in the laying hen, white mouse, and American cockroach. Jour. Econ. Ent. 49: 185–95.

Menn, J. J., W. R. Erwin, and **H. T. Gordon.** 1957. Color reaction of 2,6-dibromo-N-chloro-*p*-quinoneimine with thiophosphate insecticides on paper chromatograms. Jour. Agric. Food Chem. 5: 601–602.

O'Brien, R. D. 1957. Properties and metabolism in the cockroach and mouse of malathion and malaoxon. Jour. Econ. Ent. 50: 159–64.

[1]Accepted for publication February 11, 1959.

[2]The authors are indebted to Dr. Richard W. Young, American Cyanamid Co., Stamford, Connecticut, for the sample of malaoxon used in this study.

CHANGE OF ADDRESS

EFFECTIVE JANUARY 15, 1960

THE ADDRESS OF THE

ENTOMOLOGICAL SOCIETY OF AMERICA

WILL BE

ENTOMOLOGICAL SOCIETY OF AMERICA

4603 CALVERT ROAD

COLLEGE PARK, MARYLAND

INDEX TO VOLUME—52

All new names are printed in *italics*

Acanthococcus aceris, 402
  roboris, 402
Acarina, 1, 7, 335
Acarophenax, 336
Aceria
  ambrosiae, 142
  bowlesiae, 144
  brevisetaca, 144
  chrysothamni, 142
  cynodonis, 142
  fagerinea, 650
  nervisequus, 650
  purshiae, 144
Acomatacarus, 1, 11
Acrididae, 674
Acroceridae, 150
Acroneuria sp., 206
Aculus *copallina*, 652
Acyphoderes odyneroides, 129
Aedes aegypti
  functions of egg coverings, 113
  vitamin B. content, 26
Aedes
  hexadontus, 116
  melanimon, 528
  muelleri, 138
  sierrensis, 526
  sollicitans, 266
  taeniorhynchus, 266
  triseriatus, 138
  zoosophus, 138
Agniolamia, 565
  pardalis *camerunensis*, 566
  pardalis pardalis, 565
Agriotes mancus, molt on plant food, 535
Agromyza tritici, 22
Agromyzidae, 83, 739
Agrotis orthogonia, 198
Agulla astuta, life history and morphology, 489
Alanine in diet of Oryzaephilus surinamensis larvae, 164
Alloxacis dorsalis, study of pupae, 302
American cockroach, changes in blood proteins during development of, 733
Anagasta, pupae, 638
Anagasta kühniella, 637
Anamaspis loewi, 410
Anastrepha ludens, 192
Anepeorinae, 50
Anepeorus, 50
Anglais articae, 220
Anicetus *toumeyellae*, 29
Anopheles
  albimanus, 262
  franciscanus, 526
  freeborni, 525
  maculipennis, 116
  quadrimaculatus, 26, 214
Anopheles effect of moonlight on crucians, 261
  quadrimaculatus, 262
  walkeri, 263
Anoplius, 439
  apiculatus autumnalis, 442
  apiculatus pretiosus, 442
  atricolor, 443
  carolinus, 442
  cleora, 442
  fraternus, 440
  illinoensis, 439
  ithaca, 440
  krombeini, 440
  marginalis, 441
  marginatus, 440
  semirufus, 442
  subcylindricus, 440
  virginiensis, 440
Anthonomus grandis, morphology, 287
Anthopoda johnstoni, 655
Antiphena
  abdominalis, 129
  nigra, 129
Antron
  douglasii, 69
  echinus, 69
Aonidiella aurantii, Aphytis parasitic on, 354
Aphid, new species on sugar maple, 647
Aphid dispersal, California deserts, 368
Aphidae, 647
Aphilanthops
  (Listropygia) *bechteli*, 106
  (Clypeadon) *californica*, 108
  (Clypeadon) *dreisbachi*, 107
  (Clypeadon) *haigi*, 106
  (Clypeadon) *sculleni*, 107
Aphis
  abbreviata, growth on potatoes, 117
  gossypii, life cycle; faculative migration, 284
  sedi, 286
Aphytis, parasitic on California red scale, 354
Aphytis
  chrysomphali, 354
  citrinus, 360
  fisheri, 362
  hispanicus, 359
  lepidosaphes, 355
  lingnanensis, 360
  melinus, 361
Apis, pupae, 638
Apis mellifera, 637
Apsectus, biology and systematics, 133
Apsectus
  araneorum, 135
  dichromus, 136
  hispidus, 134
Aridaeus cleroides, 125
Arsenic trioxide, ingested, action in cockroach, 219
Ascoschöngastia, 11
Astathes
  flaviventris, 129
  posticalis, 129
Asterolecaniidae, 404
Asterolecanium
  arabidis, 404
  bellum, 404
  minus, 404
  quercicola, 404
  roboris, 404
  variolosum, 404
Astomella
  acuta, 154
  hispaniae, 153
  oldroydi, 154
  orientalis, 151
Astomelloides auripila, 156
Attenuatella (subgenus), 546
Aulacaspis rosae, 411
Auplopus, 436
  carbonarius, 438
  ochraceus, 438

Bathyplectes curculionis, interrelationships with Hypera brunneipennis in southern California, 609
Batozonellus, 438
Beauveria bassiana, pathogen of Scolytus multistriatus, 109
Beetles, hydrogen-ion concentration in alimentary canal, in stored grain, 763
Behningia, 46
  lestagei, 46
  tshernovae, 47
  ulmeri, 46
Behningiidae, 43
Belostomatidae, 93
Bembix belfragei, capturing Tabanus bishoppi, 183
Biology of
  Agulla astuta, 489
  Anopheles quadrimaculatus, 214
  Aphis gossypii, 284
  Apsectus, 132
  army cutworm, 100
  Behningiidae, 50
  Ceramidia butleri, 351
  Cryptolestes, American, 657
  Dryocosmus, 69
  Halovelia marianarum, 53
  Hyalomma anatolicum anatolicum and H. excavatum, 243
  H. excavatum, 243
  Kermes pubescens, 463
  melon aphid, life cycle, 284
  Mochlonyx cinctipes, 519
  Mycophila fungicola, 331
  Nemobius fasciatus group, 591
  nymph of Tortopus, 205
  Pasimachus punctulatus, 485
  Periplaneta americana, 570
  Pholeomyia, 316
  Sarcophaga falciformis, 724
  scale insects of Hungary, 401
  Sitophilus oryza complex, 687
  Sciomyza, 31
  Tabanus bishoppi, 183

Blaberinae, 420
Blaberus giganteus, living hemocytes in wing veins, 229
Black flies, western United States, 394
Blattaria, 420
Blattidae, 229
Blood, feeding Culex tarsalis on human, 681
Blood-cell count, variation in Periplaneta americana, 240
Blood proteins, changes in during development of Periplaneta americana, 733
Bolitotherus cornutus, 299
Bombomimus astur, 126
Bombus, 126
Book Notices: Authors:
Andarelli, L., 646
Baerg, William J., 190
Balduf, W. V., 608
Barber, Harry G., 225
Borradiale, L. A., 223
Campbell, Frank L., 551
Carthy, J. D., 646
Chamberlin, W. J., 400
Cloudsley-Thompson, J. L., 74
Eastham, L. E. S., 223
Elton, Charles S., 340
Potts, F. A., 223
Rioux, Jean A., 225
Saunders, J. T., 223
Séguy, Eugène, 62
Senevet, G., 223, 646
Strandtmann, R. W., 566
Sweetman, H. L., 224
Walker, Edmund M., 224
Wharton, G. W., 566
Book Notices: Editor:
Hubbs, Carl L., 634
Book Notices: Titles:
An Introduction to the Behavior of Invertebrates, 646
Heteroptera: Lygaeidae. Insects of Micronesia, 225
Introduction à l'Étude Biologique et Morphologique des Insectes Dipterès, 62
Les Anopheles du Globe. Revision Générale, 223
Les Culicides du "Midi" Méditerranean Étude Systématique et Écologique, 225
Les Moustiques de l'Afrique du Nord et du Bassin Médeterranéen. Les Genres Culex, Uranotaenia, Theobaldia, Orthopodomyia et Mansonia, 646
Manual of Mesostigmatid Mites, 566
Obligatory and Facultative Insects in Rose Hips, 608
Physiology of Insect Development, 551
Spiders, Scorpions, Centipedes and Mites. The Ecology and Natural History of Woodlice, "Myriapods" and Arachnids, 74
The Ecology of Invasions by Animals and Plants, 340
The Invertebrata: A Manual for the Use of Students, 223
The Odonata of Canada and Alaska. Volume II. The Anisoptera—Four Families, 224
The Principles of Biological Control, 224
The Scolytoidea of the Northwest, 400
The Tarantula, 190
Zoogeography, 634
Bracon, pupae, 638
Bracon hebetor, 637
Braconidae, 294
Byrsotria fumigata, gynandromorphs, 420

Caenis sp., 206
Calliphora, digestive enzymology, 167
Calliphora
cadaverina, 169
terrae-novae, 169
vicina, 169
vomitoria, 169
Calliphoridae, 167
Callisphyrus, 126
Calocosmus venustus, 131
Calopteron
spp., 127
textile, 128
Calopus angustus, study of pupae, 302
Campsurus, 210
Cantharoxylymma, 130
Carabidae, 485
Carulaspis visci, 412
Caudatella (subgenus), 546
Cecidophyes, 652
lyrata, 650
Cecidophyopsis, 652
Cecropia, nervous system of larva, 469
Cephalodonta maculata, 129
Cerambycidae, 552
mimetic form and coloration, 125
Ceramidia butleri, life history, 351
Ceratitis capitata, effect of temperature on eggs, 191
Ceratopogonidae, 617
Chaetococcus phragmitis, 402
Chalcididae, 75
Chatia, 10
furmani, 8
Cheladonta, 11
crossi, 15
micheneri, 15
michneri, 15
Cheumatopsyche sp., 206
Chionaspis
lepineyi, 411
salicis, 411
Chironomidae of Alabama, 506
Chitinophora (subgenus), 544
Chloridolum, 129
Chlorophorus (Clytanthus) annularis, 129
Choristoneura fumiferana, 605
Chorizagrotis auxiliaris, development and behavior, 100
Chortinaspis subterraneous, 412
Cicadellidae, 304
Cimicidae, 81
Clover root borer, studies of vertical distribution in red clover, 760
Clypeadon (subgenus), 105
Clytini, Batesian mimicry in, 125
Coccidae, 404
Coccoidea, 463
Cockroach, peripheral distribution of thoracic nerves of Periplaneta americana, 695
Cockroaches, blood toxins in DDT-poisoned, 386
Coelotanypus concinnus, 510
Coleoptera, 125, 164, 173, 287, 299, 485, 503, 534, 537, 540, 609, 657
Colorhombus
auricomus, 126
fasciatipennis, 126
Comatacarus, 10
Comperiella bifasciata, 355
Compsosoma mutillarium, 128
Cordiseta mexicana, 11
Corn borer moths, influence of development of dent corn on oviposition, 272
Corydalus cornutus, 206
Cottophylla, 652
Cricotopus
belkini, 510
trifasciatus, 510
Cryptocheilus, 434
Cryptococcus fagisuga, 402
Cryptolestes, bionomics of American, 657
Cryptolestes
ferrugineus, 657, 763
minutus, 657
pusilloides, 657
turcicus, 657, 763
Ctenicera aeripennis aeripennis, growth and feeding behavior of larvae, 540
aeripennis aeripennis, growth and survival, 537
aeripennis destructor, rearing larvae, 173, 540
tarsalis, compared with noncannibals, 534
Ctenodes, 130
Cucujidae, 657
Culex
fatigans, vitamin B content, 26
molestus, vitamin B content, 26
nigripalpus, 263
pipiens, 525
pipiens, vitamin B content, 26
pipiens fatigans, 116
stigmatosoma, 526
tarsalis, 481, 524, 681, 767
Culicidae, 137, 345, 481, 519, 524, 668
Culicoides
actoni, 627
alatus, 617
anophelis, 624
autumnalis, 628
candidus, 620
clavipalpis, 620
daleki, 624
definitus, 622
distinctus, 618
dumdumi, 628
fortis, 622
fulvithorax, 625
fulvus, 628
himalayae, 617
indianus, 627
inexploratus, 628
iniquus, 620
innoxius, 626
kamrupi, 617
macfiei, 625
magnificus, 622
minutus, 622
odiosus, 624
orientalis, 627
oxystoma, 624
palpifer, 625
pattoni, 624
peregrinus, 627
peregrinus assamensis, 627
raripalpis, 626
shortti, 626
similis, 618
studies on Indian, 617
turgidus, 626
Culiseta
incidens, 526
inornata, 526
maccrackenae, 526
Curculionidae, 287, 609

Cyclocranium swierstrae, 126
Cylindrepomus comis, 129
Cynipidae, 69
Cyphus myrmosarius, 128
Cyrtus
kashmirensis, 158
orbifer, 158

Dactylopiidae, 463
Dacus, effect of temperature on eggs, cucurbitae, 191
dorsalis, 191
Dannella (subgenus), 546
Daphisia sp., 129
Dasyhelea setiger, 628
DDT, effect of on respiratory enzymes of mealworm and house fly, 179
DDT-poisoned cockroaches, blood toxins, 386
Deinocerites cancer, 266
Delpyiella (subgenus), 243
Demonax, 129
Dendroides
canadensis, 299
concolor, 299
ephemeroides, 299
Dent corn, influence of oviposition by European corn borer moths, 272
Diaspididae, 408
Diaspidiotus
alni, 416
bavaricus, 416
hungaricus, 416
wünni, 416
Diplura, Japygidae of North America, 363
Dipogon, 434
intermedius, 436
papago anomalus, 436
sayi sayi, 436
variegatus, 436
Diptacus
fragarifoliae, 656
rubra, 656
Diptera, 17, 31, 83, 121, 137, 150, 167, 183, 316, 331, 345, 394, 444, 481, 506, 519, 524, 617, 668, 724, 728, 739
Ditylus quadricollis, study of pupae, 302
Dolania americana, 46
Dolichocybe keiferi, 336
Dolichoderus
mariae, 759
(Hypoclinea) taschenbergi, flight activities, 755
Doliops curculionoides, 129
Drepanaphis
acerifoliae, 647
simpsoni, 647
Drosophila, pupae, 638
Drosophila melanogaster, 637
Drunella (subgenus), 546
Dryocosmus, heterogony, 69
Dryocosmus
bicornis, 69
dubiosus, 69
minusculus, 72
Dynaspidiotus abietis, 412

Ecological studies, melon leaf miner, 83
Ecology of dark rice field mosquito, 345
Elateridae, 173, 534, 537, 540
Empoasca
anilla, 315
arvalis, 313
beckeri, 310
canda, 310
cunninghami, 314
eccla, 316
fabae, complex, 304, 315
fenestra, 312
gansella, 312
gibsoni, 314
hastosa, 314
incoata, 313
kraemeri, 311
loreta, 313
mergata, 312
mexara, 315
millsi, 315
panisca, 315
tetronis, 313
verdia, 315
zapoides, 310
Encyrtidae, 28
Epania
sarawakensis, 128
singaporensis, 128
Ephemera, 206
Ephemerella, subgeneric groups, 543
Ephemerella (Drunella)
allegheniensis, 546
atagosana, 546
(*Attenuatella*) attenuata, 546
(Chitinophora) aurivillii, 544
(Drunella) autumnalis, 546
(Drunella) basalis, 546
(Torleya) belgica, 546
(Chitinophora) berneri, 544
(Eurylophella) bicolor, 546
(Eurylophella) bicoloroides, 546
(Chitinophora) catawba, 544
(Drunella) cherokee, 546
(Chitinophora) choctawhatchee, 544
(*Serratella*) cognata, 545
(Drunella) coloradensis, 546
(*Caudatella*) columbiella, 546
consimilis, 546
(Drunella) cornuta, 546
(Drunella) cornutella, 546
(Drunella) cryptomeria, 546
(*Serratella*) deficiens, 545
(*Attenuatella*) delantala, 546
(Drunella) depressa, 546
(Drunella) doddsi, 546
(Eurylophella) doris, 546
(Ephemerella) dorothea, 544
(*Caudatella*) edmundsi, 546
elongatula, 546
(Chitinophora) euterpe, 544
(Ephemerella) excrucians, 544
(Drunella) flavilinea, 546
(Drunella) flavitincta, 546
(Ephemerella) fratercula, 544
(*Serratella*) frisoni, 545
(Eurylophella) funeralis, 546
(Drunella) glacialis, 546
(Drunella) glacialis carsona, 546
gracilis, 546
(Drunella) grandis, 546
(Timpanoga) hecuba, 546
(Timpanoga) hecuba hecuba, 546
(Timpanoga) hecuba pacifica, 546
(*Caudatella*) heterocaudata, 546
(*Attenuatella*) hirsuta, 546
hispanica, 546
(Caudatella) hystrix, 546
(Chitinophora) ignita, 544
(Drunella) ingens, 546
(Ephemerella) inconstans, 544
(Ephemerella) inermis, 544
(Ephemerella) infrequens, 544
(Ephemerella) invaria, 544
(Drunella) ishiyama, 546
(*Caudatella*) jacobi, 546
(Eurylophella) karelica, 546
(Chitinophora) krieghoffi, 544
(Ephemerella) lactata, 544
(Drunella) lapidula, 546
(Drunella) lata, 546
(Drunella) latipes, 546
lenoki, 546
(*Serratella*) levanidovae, 545
(*Dannella*) lita, 546
(Eurylophella) lodi, 546
(*Serratella*) longicaudata, 545
(Drunella) longicornis, 546
longipes, 546
(Eurylophella) lutulenta, 546
(Chitinophora) maculata, 544
(Torleya) major, 546
(*Attenuatella*) margarita, 546
(Chitinophora) mesoleuca, 544
(*Serratella*) micheneri, 545
(Eurylophella) minimella, 546
(*Serratella*) molita, 545
(Ephemerella) mollitia, 544
(Chitinophora) needhami, 544
nigra, 546
(Chitinophora) notata, 544
(Ephemerella) ora, 544
(*Serratella*) orientalis, 545
(Drunella) pelosa, 546
(Drunella) proserpina, 546
(Eurylophella) prudentalis, 546
(Drunella) punctisetae, 546
quebecensis, 546
(Ephemerella) rotunda, 545
rufa, 546
sachalinensis, 546
(Chitinophora) septentrionalis, 546
(Ephemerella) septentrionalis, 544
(*Serratella*) serrata, 544
(*Serratella*) serratoides, 545
(Chitinophora) sibirica, 544
(Drunella) sierra, 546
(*Dannella*) simplex, 546
sinensis, 546
(*Attenuatella*) soquele, 546
(*Serratella*) sordida, 545
(Drunella) spinifera, 546
submontanus, 546
(Ephemerella) subvaria, 544
(Chitinophora) sven-hedini, 544
taeniata, 546
(Eurylophella) temporalis, 546
(Drunella) tenax, 546
(*Serratella*) teresa, 545
thymalli, 546
(*Serratella*) tibialis, 545
(Ephemerella) torrentium, 544
(Drunella) triacantha, 546
(Eurylophella) trilineata, 546
(Drunella) trispina, 546
(Drunella) tuberculata, 546
(Eurylophella) versimilis, 546
(Drunella) wayah, 546
unicornis, 546
(Drunella) wilsoni, 546
(Ephemerella) argo, 544
Ephemerellidae, 543
Ephemeroidea, 43
Ephemeroptera, 43, 205, 543
Ephoron, 206
Epidiaspis leperii, 412
Epilachna varivestis, 637
Epimellita, 130
Episomus chlorostigma, 128
Episyron
posterus, 439
quinquenotatus quinquenotatus, 439

Epitrimerus
demissae, 655
virginiana, 654
Eriopeltis festucae, 404
Eriophyes *arida*, 148
Erotylus sexfasciatus, 128
Erythroplatys corallifer, 129
Estigmena chinensis, 128
Estigmenida variabilis, 128
Eucalliphora lilaea, digestive enzymology, 167
Eulecanium
arion, 404
bituberculatum, 404
ciliatum, 404
corni, 404
crudum, 407
franconicum, 407
persicae, 407
prunastri, 407
rufulum, 408
Eulophidae, 354
European corn borer, population fluctuations in Minnesota, 710
Eurygarka helicis, 450
Eurygenius campanulatus, 299
Eurylophella (subgenus), 546
Eurystethus debilis, 299
Euschöngastia, 11
(Ascoschöngastia) anomala, 15
bigenuala, 14
blarinae, 14
californica, 14
campi, 14
carolinensis, 14
citellicola, 14
cordiremus, 14
crateris, 14
criceticola, 14
cynomyicola, 14
decipiens, 14
diversa acuta, 14
diversa diversa, 14
enemi, 14
fasolla, 14
finleyi, 13
frondifera, 14
furmani, 14
guntheri, 14
hamiltoni, 14
hoffmannae, 14
jonesi, 14
lacerta, 13
lanceolata, 14
lanei, 14
loomisi, 14
luteodema, 15
magna, 14
marmotae, 14
micheneri, 14
nihi, 15
nunēzi, 13
obesa, 14
ohioensis, 14
oregonensis, 14
(Ascoschöngastia) pedregalensis, 15
peromysci, 14
pipistrelli, 14
pomerantzi, 15
puerilis, 14
radfordi, 14
romola, 15
rotunda, 14
rubra, 14
sciuricola, 14
setosa, 14
soricinus, 14
trigenuala, 14
utahensis, 14
Eutrombicula, 10
Eye gnat, flight range, dispersal patterns, and population density, 641

Fonsecia palmella, 10
Formicidae, 176, 755
Fruit flies, effect of temperature environments on egg development, 191

Gahrliepia, 11
(Walchia) americana, 12
(Walchia) gouldi, 12
Galleria mellonella, 637
Glenea iresine, 128
Glyptacus, 652
Glyptotendipes
meridionalis, 517
paripes, 517
Gossyparia spuria, 402
Grabhamia, taxonomical studies on larvae of common species, 668
Grapholitha molesta, 637
Grasshoppers, a parasite of, 724
Gryllidae, 591
Guanase, from Leucophaea maderae, 548
Gymnocerus
belti, 130
dulcissimus, 130
Gynandromorphs of Byrsotria fumigata, 420

Habrobracon, antimitotic substances fed to female, 294
Habrobracon juglandis, 637
Haemagogus equinus, 137
Halovelia marianarum, biology of, 53
Hannemania, 10
dunni, 11
eltoni, 11
hegeneri, 11
hylae, 11
Haplothrips clarisetis in southern California, 765
Hecajapyx vulgaris, 366
Hemipepsis ustulata ochroptera, 432
Hemiptera, 81, 93, 279, 304
Hemocytes in wing veins of cockroach, 229
Hertigia hertigi, 122
Heterogeny, Dryocosmus, 69
Heterops dimidiata, 130
Heteroptera, 53
Hexapod, studies on nervous system, 695
Hippelates collusor, 641
Hippelates pusio, dispersal of adult, 372
Hoffmanina suriana, 8
Holly, Torymus from seeds, 52
Homonotus sanguinolentus, 443
Homoptera, 463, 647
Hornworms, natural enemies of, on tobacco, 741
Human hosts, effects on Mansonia perturbans, 236
Hyalomma
anatolicum, 243
anatolicum anatolicum, 244, 248, 257
anatolicum excavatum, 248, 250, 254, 256
excavatum, 244
franchinii, 254
hussaini, 243
lusitanicum, 244, 256
marginatum, 247
rhipicephaloides, 244
ticks, Egyptian, biological notes, 243
truncatum, 247
Hyalommina (subgenus), 243
Hylastinus obscurus, 760
Hylotoma pruinosa, 128
Hymenoptera, 28, 52, 69, 75, 105, 176, 294, 354, 430, 609, 755
Hypera brunneipennis, interrelationships with Bathyplectes curculionis in southern California, 609

Ichneumonidae, 609
Insect
epicuticle and terminology, 381
fat body, oxidative metabolism, 567
Insects
oxygen poisoning in, 637
scale, of Hungary, biological notes, 401
Ipochus, 126
Isonychia sp., 206
Ites, 128
Itonididae, 331
Ixais castelnaudi, 128

Japygidae of North America, 363
Johnella, 650
chrysolepis, 652
virginiana, 652

Kermes pubescens, life history and morphology, 463
Kermococcus
quercus, 402
roboris, 404

Lasia aurata, 158
Leeuwenhoekia (Comatacarus) americana, 11
dolosa, 11
stewarti, 11
Lepidospychoda, 447
tineiformis, 447
trimicra, 448
Lepidoptera, 100, 351, 469, 741
Lepidoptera, furcopleural muscles, 665
Lepidosaphes
conchyformis, 410
granati, 410
newsteadi, 410
ulmi, 410
Leptotrombidium, 10
Leptura sp., 129
Lepturini, Batesian mimicry in, 125
Lesbra graueri, 564
Lethocerus, locomotion, 93
Leucaspis
pini, 408
pusilla, 410
Leucophaea maderae, 548
Limonius agonus, predation and survival, 534
Liriomyza pictella, 83, 739
Listropygia (subgenus), 106
Locomotion of Lethocerus, 93
Locusta migratoria, 220
Loxaulus trizonalis, 69
Lycidola retifera, 128
Lycomimus albocinctus, 128
Lyctus planicollis, influence of environment on development, 632
Lycus, 126
Lygaeidae, 279
Lygesis, 128

Macromerus splendida, 126
Macronemum carolina, 206
Macrosiphum solanifolii, growth on potatoes, 117

Melathion metabolism in larvae of resistant mosquito strains, 767
Mansonia effect of moonlight on
indubitans, 263
perturbans, 261
Mansonia perturbans, localizing effects of human hosts, 236
Megachile, 130
Melandrya striata, 299
Melanolamia, 554
albosignata, 555
melaleuca, 555
Melanoplus
bilituratus, utilization of food plants by, 674
devastator, 724
mexicanus, 198, 674
Melanopolia, and allies, Ethiopian, 552, 556
Melanopolia
brevicornis, 563
catori catori, 562
catori *vittata*, 563
cincta cincta, 557
cincta *camerunensis*, 558
cotytta, 560
frenata, 559
freundei, 560
latisfasciata, 561
ligata, 561
ligondesi, 564
longiscapa, 563
lysida, 557
maculata, 564
nubilosa, 558
Melanotus, compared with cannibalistic Coleoptera, 534
Melipona vidua, 128
Melon leaf miner, host range studies, 739
Melzerella lutzi, 128
Meoneura, 18
alpina, 24
digitata, 19
elongella, 25
flavifacies, 24
forcipata, 24
glaberrima, 22
lamellata, 23
neglecta, 22
nigrifrons, 25
nitidiuscula, 22
obscurella, 22
palaestinensis, 22
perlamellata, 24, 25
polita, 20
pteropleuralis, 19
seducta, 22
triangularis, 24
vagans, 23
wirthi, 25
Mesolita inermis, 126
Methia, 126
Methods
enzyme, on oxidative metabolism of insect fat body, 567
for characterizing toxin in DDT-poisoned cockroaches, 386
for conducting ecological studies of Liriomyza pictella, 83
for conducting experiments with feeding whole blood to Culex tarsalis, 682
for conducting investigation of action of arsenic trioxide in Periplaneta americana, 219
for conducting survey for pathogens of Scolytus multistriatus, 109
for determining alanine and proline requirements of Oryzaephilus surinamensis, 164
for determining aphid dispersal over California deserts, 368
for determining blood-cell count of Periplaneta americana, 240
for determining changes in size of mosquito populations, 346
for determining developmental serum protein changes in Periplaneta americana, 734
for determing effect of temperature on egg development of fruit flies, 191
for determining effects of DDT on Tenebrio molitor and Musca domestica, 179
for determining effects of sterilized soil on Ctenicera larvae, 538
for determining efficiency of sticky traps in sampling Aceria tulipae, 160
for determining growth of Ctenicera larvae, 540
for determining host range of Liriomyza pictella, 739
for determining influence of dent corn on oviposition by corn borer moths, 272
for determining influence of Tribolium confusum on microflora, 452
for determining oxidative metabolism of insect fat body, 567
for determining survival of Pyrausta nubilalis in artificial tunnels in stalks of field corn, 631
for determining population changes in Pyrausta nubilalis, 711
for determining treatment perimeter and directions of flight of eye gnat, 641
for determining strength-weight relationship within Tenebrio molitor, 766
for determining whether Culex tarsalis larvae converted malathion to its oxygen analog, 767
for field sampling of Hypera brunneipennis and Bathyplectes curculionis, 609
for investigation continuance on Culex tarsalis, 524
for isolating enzymes from fat body of Leucophaea maderae, 548
for observing blood circulation in wings of Blaberus giganteus, 229
for observing changes in biology of Anopheles quadrimaculatus, 214
for rearing Agulla astuta, 489
for rearing larvae of Ctenicera, 173
for redescribing Pygostenini, 503
for study of eggs of Culex tarsalis, 481
for study of Solenopsis saevissima richteri, 573
for study of oxygen poisioning in insects, 637
for study of thoracic nerves of Periplaneta americana, 696
for study of utilization of food plants by Melanoplus bilituratus, 674
for obtaining frass samples of spruce budworm, 606
for study of measure of effect on hornworm populations of enemies that kill eggs and larvae, 741
for study of relation between seasonal progression and vertical distribution of clover root borer, 761
for study of reproductive systems of cotton boll weevil, 287
of investigating the gut in beetles in relation to their feeding on stored cereals, 763
of nomenclature and illustration of nervous system of Cercropia larva, 471
of observing flights of Dolichoderus, 755
of testing predation and survival of Limonius agonus, 534
Michthysoma, 127
Microbracon hebetor, feeding antimitotic substances, 294
Microcleptes variolosus, 126
Micropsectra dubia, 513
Migratory grasshopper, utilization of food plants by, 674
Miliichia proectes, 317
Milichiidae, 17, 316
Milkweed bug, hygroreceptors, 279
Mimetic form and coloration in Cerambycidae, 125
Mites, new eriophyid, 649
Miyatrombicula kochiensis, 13
Mochlonyx cinctipes, life history, 519
Molorchus, 126
Monochamidi, 552
Monochamini of Ethiopian region, 552
Morphology
Agulla astuta, 500
cotton boll weevil, 287
embryos of Culex tarsalis, 481
Kermes pubescens, 463
poison glands and sting of Solenopsis saevissima richteri, 573
Mosquito strains, malathion metabolism in larvae of resistant, 767
Mosquitoes
dark rice field, ecology, 345
floodwater, functions of coverings of eggs, 113
influence of moonlight on light-trap catches, 261
localizing effects of human hosts, 236
vitamin B content, 26
Musca domestica, effects of DDT on respiratory enzymes, 179
Musca domestica, 637
Mycophila fungicola, redescription and review of biology, 331
Mygnimia ptinceps, 126
Myosoma, 127
Myzus
persicae, growth on potatoes, 117
solani, growth on potatoes, 117

Nacerdes melanura, study of pupae, 302
Nanocladius *alternantherae*, 510
Necydalini, Batesian mimicry in, 125
Necydalis, 126
Nemobiinae, 591
Nemobius
allardi, 592
fasciatus group, 591
tinnulus, 592
Neopanops boharti, 157
Neopyrochroa femoralis, 299
Neoschöngastia, 11
americana, 15
brennani, 15

fullbergae, 15
paenitens, 15
Neotrombicula, 10
Neuroptera, 489
Newsteadia floccosa, 402
Nigrolamia, 552
borussa, 553
ogowensis, 553
farinosa, 554
Noctuidae, 100
Novotrombicula suriana, 8

Oberea, 127
Obituaries:
Needham, James George, 338
Gerhard, William J., 338
Occasjapyx, 363
californicus, 363
sierrensis, 363
silvestri, 363
Ochrya nana, 126
Odontacarus, 1
arizonensis, 11
australis, 2
bakeri, 11
brevicalcar, 11
cayolargoensis, 2, 11
chiapanensis, 11
dentatus, 1
galli, 11
hirsutus, 11
linsdalei, 11
micheneri, 11
morlani, 4, 11
plumosus, 11
polychaetus, 11
shawi, 5
whartoni, 11
Odontocera, 130
Oedaleonotus enigma, 727
Oedemera virescens, study of pupae, 302
Oedemeridae, study of pupae, 299
Ommata spp., 130
Oncopeltus fasciatus, antennal hygroreceptors, 279
Oregostoma luridum, 130
Ornistomis, 130
Orthezia urticae, 401
Ortheziidae, 401
Orthopodomyia
alba, first instar larvae, 137
anopheloides, 141
californica, 141
fascipes, 141
signifera, first instar larvae, 137
Orthoptera, 229, 591, 674
Oryzaephilus
mercator, 763
surinamensis, 164, 763
Othnius umbrosus, 299
Oxycopis, study of pupae
suturalis, 302
thoracica, 302
Oxylymma, 130

Pachyrrhynchus erischsoni, 129
Palingenia, 206
Palpomyia, 206
Panops baudini, 154
Papilio machaon, 666
Paralauterborniella elachistus, 513
Paraphytoptus *artemisiae*, 148
Paratendipes basidens, 513
Pasimachus punctulatus, courtship and copulation, 485
Pavania, 336
Pediculus humanus corporis, 279
Pelopia punctipennis, 509
Pentaneura
aequifasciata, 507
annulata, 508
basalis, 508
aspera, reactions to sound, 728
carnea, 507
cinctipes, 508
idei, 508
illinoensis, 508
mallochi, 508
monilis, 206, 508
peleensis, 508
prudens, 508
Pepsis, 431
mexicana, 431
thisbe, 431
Periplaneta americana
biology and dehydrogenase activities of fat body, 570
blood toxins in DDT-poisoned, 386
changes in blood proteins during development of, 733
ingested arsenic trioxide, 219
oxidative metabolism of fat body, 567
peripheral distribution of thoracic nerves, 695
variation in blood-cell count, 240
Phaenicia sericata, digestive enzymology, 167
Phespia corinna, 130
Philosepedon, 448
bishoppi, 449
distyla, 449
flavithorax, 449
humeralis, 449
interdicta, 449
maderensis, 449
malayensis, 449
mayeri, 449
opposita, 449
tesca, 449
triangulata, 449
triastyla, 449
tridactila, 449
Phlaeothripidae, 765
Phlebotomus
distribution in Central America, 121
species between Panama and U. S., 121
Phlebotomus
aclydiferus, 121
anduzei, 121
anthophorus, 121
apicalis, 121
arborealis, 121
barrettoi, 121
bispinosus, 121
camposi, 121
carpenteri, 121
cayennensis, 121
cayennensis maciasi, 121
chiapanensis, 122
cruciatus, 122
ctenidophorus, 122
cunhai, 122
deleoni, 122
del pozoi, 122
diabolicus, 122
dodgei, 122
durani, 122
dysponetus, 122
evansi, 122
galindoi, 122
gomezi, 122
hardisoni, 122
intermedius, 122
longipalpis, 122
oppidanus, 122
ovallesi, 122
panamensis, 122
paraensis, 122
permirus, 122
pilosus, 122
sanguinarius, 122
saulensis, 122
shannoni, 122
steatopygus, 122
stewarti, 122
texanus, 122
trapidoi, 122
trinidadensis, 122
undulatus, 122
vesiciferus, 122
vespertilionis, 122
vexator, 122
vindicator, 122
viriosus, 122
wirthi, 122
ylephiletor, 122
Pholeomyia, revision of genus, 316
Pholeomyia
comans, 330
dampfi, 328
decorior, 324
dispar, 327
expansa, 323
hurdi, 324
indecora, 322
latifrons, 321
leucogastra, 326
longiseta, 321
pseudodecora, 326
leucozona, 329
myopa, 325
nitidula, 327
obscura, 330
politifacies, 323
robertsoni, 328
texensis, 329
Phormia
regina, 167, 637
Phryganidia californica, 69
Phyllocoptes *sassafrasella*, 654
Physopoda
albitarsis, 130
subvestita, 130
Pialea auripila, 156
Pieris brassicae, 220
Papilio glaucus glaucus, 486
Pitomba, 130
Pleurocera sp., 206
Poecilopompilus, 438
interruptus interruptus, 438
Pogonomyrmex occidentalis, Batesian mimicry similarilty to Veromessor lobognathus, 176
Polybia
liliacea, 129
nigra, 129
Polymitarcidae, 205
Polymitarcys virgo, 206
Polypedilum
digitifer, 513
illinoensis, 513
parvum, 513
scalaenum, 513
simulans, 513
trigonus, 513
Polystomophora ostiaplurima, 402
Pompilidae, larvae, 430
Porthetria dispar, 220

Potamyia flava, 206
Povilla adusta, 207
Priocnemis, 434
  cornica, 434
  minorata, 434
Procladius culiciformis, 510
Prodenia, 220
  eridania, 637
Proline in diet of Oryzaephilus surinamensis larvae, 164
Prospaltella perniciosi, 355
Protocalliphora
  avium, digestive enzymology, 167
  regina, 169
  sericata, 169
  terrae-novae, 169
Protoparce
  quinquemaculata, 741
  sexta, 741
Protophormia terrae-novae, digestive enzymology, 167
Psebena brevipennis, 128
Psectrocladius vernalis, 513
Pseudaulacaspis pentagona, 412
Pseudochermes fraxini, 402
Pseudococcidae, 402
Pseudoschöngastia, 11
  diazi, 15
  farneri, 15
  hungerfordi, 15
  occidentalis, 15
Pseudosida bidentata, 199
Psilodera
  aurata, 158
  orbifer, 158
Psorophora, 267, 668
  (Psorophora) ciliata, 668
  confinnis, 268
  confinnis, notes on ecology in Coachella Valley, California, 345
  (Grabhamia) confinnis, 668
  (Janthinosoma) cyanescens, 668
  (Grabhamia) discolor, 668
  (Janthinosoma) ferox, 668
  (Janthinosoma) horrida, 668
  (P.) howardii, 668
  (Janthinosoma) johnstonii, 668
  (Janthinosoma) longipalpis, 668
  (Grabhamia) pygmaea, 669
  (Grabhamia) signipennis, 668
  (Janthinosoma) varipes, 668
Psychoda, 450
  alternata, 447
Psychodidae, 121, 444
Psychodini, classification, 444
Pteracantha, 130
Pterocallidium (subgenus), 63
Peterodontia
  dorsolineata, 158
  kashmirensis, 158
Pteroplatini, Batesian mimicry in, 125
Pteroplatus spp., 127
Pulvinaria
  artemisiae, 408
  betulae, 408
Purshia glandulosa, 149
Pyemotes, 336
  ventricosus, 335
Pyemotidae, notes on, 335
Pygmephorus, 336
Pygostenini, little-known, 503
Pygostenus magnus, 504
Pyrausta nubilalis
  influence on dent corn oviposition, 272
  population fluctuations in Minnesota, 710
  survival in artificial tunnels of field corn, 631
Pytho americanus, 299

Quadraspidiotus
  gigas, 412
  lenticularis, 414
  marani, 414
  ostreaeformis, 414
  perniciosus, 414
  pyri, 415
  sulci, 415
  zonatus, 415

Radiotracer labeling of tephritid population, 90
Raphidiidae, 489
Raphidiodea, 489
Resinacarus resinatus, 336
Rhagoletis completa, flight range, 90
Rhathymoscelis peruibensis, 128
Rhinotragini, Batesian mimicry in, 125
Rhinotragus opicalis, 130
Rhizoberlesia trifolii, 68
Rhizococcus obscurus, 402
Rhysogaster, 150
  implicata, 151
  indica, 151
  orientalis, 151
  panayensis, 152
Rhizopertha dominica, 763
Rhyncaphytoptus *rubrifoliae*, 656
Rice weevil, biological study of complex, 687

Saissetia oleae, Agulla astuta reared on eggs and crawlers, 489
Salius ceylonicus, 126
Sarcophaga
  bullata, 169
  cooleyi, 169
  falciformis, 724
  shermani, 169
Sarcophagidae, 167, 724
Sasacarus furmani, 8
Saturniidae, 469
Schizotus cervicalis, 299
Sciomyza
  aristalis, 32
  dryomyzina, 40
  simplex, 40
  snail-killing flies of genus, 31
  varia, 43
Sciomyzidae, 31
Scolytus multistriatus, Beauveria bassiana as a pathogen of, 109
Serratella (subgenus), 544
Serropalpus barbatus, 299
Sessinia livida, study of pupae, 302
Shunsennia, 10
Silvanidae, 164
Simuliidae, 394
Simulium
  petersoni, 394
  wyomingensis, 395
Siteroptes, 336
  reniformis, redescription of male, 335
Sitophilus
  granarius, 763
  oryza, biological study, 687
  sasakii, 689
Solenopsis saevissima richteri, poison glands and sting, 573
Spathomeles, 127
Speleocola tadaridae, 10
Sphaerium sp., 206
Sphecidae, 105
Sphecomorpha murina 129
Sphingidae, 741
Spinosomatidia, 126
Spruce budworm larval instars, frass size indicator, 605
Staphylinidae, 503
Stenelmis sp., 206
Stenochironomus
  hilaris, 514
  macateei, 514
Stenonema sp., 206
Sternacanthus undatus, 128
Sticky traps in sampling mite populations, 159
Stictochironomus palliatus, 514
Streptolabis, 130
Stricticimex *intermedius*, 81
Sympolemon rufobrunneus, 503
Synchroa punctata, 299
Syntomidae, 351

Tabanidae, 183
Tabanus
  affinis aurilimbus, 184
  bishoppi, hovering and mating, 183
Tanytarsus
  confusus, 513
  neoflavellus, 513
  viridiventris, 513
Targionia vitis, 416
Tarsonemoides termitophilus, 336
Tecomatlana, 10
Temperature environments, effect on egg development of fruit flies, 191
Tendipedidae, 506, 728
Tendipes
  amachaerus, 516
  atrimanus, 514
  brachialis, 514
  brunneipennis, 514
  crassicaudatus, 514
  decorus, 514
  directus, 514
  fulvipilus, 514
  fulvus, 516
  fuscicornis, 514
  modestus, 514
  monochromus, 516
  nervosus, 514
  nigricans, 514
  pectinatellae, 516
  plumosus, 514
  tenuicaudatus, 516
Tenebrio molitor, 179, 637, 766
Tephritid population, radiotracer labeling, 90
Termitadelphos, 451
Tetraopes, 130
Therioaphis
  maculata, 63, 368
  trifolii, 63
Thretricus, 449
  aenigmaticus, 450
  bicolor, 450
  dubitatus, 450
  irroratus, 450
  jonesi, 450
  lucifugus, 450
  philpotti, 450
  unimaculatus, 450
Thysanoptera, 765
Tiger swallowtail butterfly, flight behavior, 486
Tillomorphini, Batesian mimicry in, 125

Timpanoga (subgenus), 546
Tomopterus larroides, 130
Torleya (subgenus), 546
Tortopus
  circumflus, 210
  incertus, 206
  manitobensis, 210
  primus, 210
Torymidae, 52
Torymus
  fullawayi, 74
  rugglesi, 52
Toumeyella liriodendri, 28
Toxorynchites rutilis septentrionalis, 137
Toxoptera graminum, 368
Tribolium
  castaneum, 763
  confusum, 452, 763
Trichopsychoda, 446
  africana, 447
  boninensis, 447
  carolinensis, 447
  hirtella, 447
  insulicola, 447
  montana, 447
Trichrous, 130
Tricorythodes sp., 206
Trigonura, 75
  algerti, 77
  californica, 76
  elegans, 78
  hicoriae, 78
  pini, 80
  tarsata, 77
  ulmi, 80
Trinodinae, characterized, 132
Trisetacus *grosmanni*, 649
Trogodendron fasciculatum, 125
Trogoderma
  parabile, 763
  versicolor, 763
Trombicula, 11
  (Eutrombicula) alfreddugesi alfreddugesi, 12
  (Eutrombicula) alfreddugesi tropica, 12
  allredi, 12
  aplodontiae, 12
  arenicola, 12
  (Neotrombicula) autumnalis, 13
  azteca, 12
  bakeri, 12
  (Eutrombicula) batatas, 12
  (Eutrombicula) belkini, 12
  beltrani, 12
  (Neotrombicula) bisignata, 13
  boneti, 12
  (Neotrombicula) brennani, 13
  browni, 13
  (Neotrombicula) californica, 13
  (Neotrombicula) carterae, 13
  (Neotrombicula) cavicola, 13
  crossleyi, 12
  (Miyatrombicula) cynos, 13
  (Neotrombicula) dinehartae, 13
  doremi, 12
  (Miyatrombicula) esoensis, 13
  (Neotrombicula) eusignata, 13
  (Neotrombicula) finleyi, 13
  fitchi, 12
  (Neotrombicula) goodpasteri, 13
  gurneyi, 12
  gurneyi campestris, 12
  (Neotrombicula) harperi. 13
  hoplai, 12
  jamesoni, 7, 10, 12
  jessiemae, 12
  (Neotrombicula) jewetti, 13
  (Miyatrombicula) jonesae, 13
  kansasensis, 12
  kardosi, 12
  (Eutrombicula) lipovskyana, 12
  (Neotrombicula) lipovskyi, 13
  (Neotrombicula) loomisi, 13
  merrihewi, 12
  (Neotrombicula) mexicana, 13
  (Neotrombicula) microti, 13
  montanensis, 12
  (Eutrombicula) multisetosa, 12
  (Leptotrombidium) myotis, 12
  nativitatis, 12
  ornata, 12,
  (Leptotrombidium) panamensis, 13
  (Neotrombicula) pomeranzevi, 13
  (Leptotrombidium) potosina, 13
  (Neotrombicula) pseudoautumnalis, 13
  (Neotrombicula) richmondi, 13
  (Miyatrombicula) sargenti, 13
  (Miyatrombicula) scottae, 13
  sola, 12
  (Eutrombicula) splendens, 12
  (Neotrombicula) subsignata, 13
  (Neotrombicula) sylvilagi, 13
  trisetica, 12
  (Neotrombidium) twentei, 13
  (Neotrombicula) varians, 13
  (Neotrombicula) waynesis, 13
  (Neotrombicula) whartoni, 13
Trombiculida 7
Tropidosoma, [illegible]

Ulochaetes leoninus, 126
Unaspis euonymi, 411
Uranotaenia sapphirina, 266
Uricase, from Leucophaea maderae, 548

Veliidae, 53
Veromessor lobognathus, second note, 176
Vitamin B content of mosquitoes, 26
Volucella pusilla, indifference of Tabanus bishoppi toward, 190

Walchia, 11
Walnut husk fly, flight range, 90
Warileya rotundipennis, 122
Whartonia, 10
  nudosetosa, 11
  perplexa, 11
  senase, 11
  whartoni, 11
Winthemia n. sp., 744
Wohlfartia opaca, digestive enzymology, 167
Womersia strandtmani, 10

Xanthine oxidase, from Leucophaea maderae, 548
Xanthochroa erythrocephala, 302
Xyaste, 127
Xylotrechus, 129

Zelota sphathomelina, 127
Zopherus haldemani, 299
Zygosturmia protoparcis, 744

PREPUBLICATION ANNOUNCEMENT
ANNUAL REVIEW OF ENTOMOLOGY

VOLUME 5

EDITORS: EDWARD A. STEINHAUS and RAY F. SMITH

Editorial Committee: P. A. DAHM, ROBERT GLEN, H. H. ROSS, L. E. ROZEBOOM, R. F. SMITH, E. A. STEINHAUS, C. M. WILLIAMS

Volume 5 of this series will be published in January 1960. The four previous volumes, which are still available, established the high standards of the ANNUAL REVIEW OF ENTOMOLOGY.

Members of the Entomological Society of America: Your order is to be placed with our Washington office. You will receive an order blank through the mail. Member's price is given on the order blank. Every member should have a copy.

TABLE OF CONTENTS

Physiology of Excretion . . . . . R. Craig
Flight Muscles and Their Basic Physiology . . . . . E. G. Boettiger
Insect Micromorphology . . . . . George A. Edwards
Phylogeny of Coleoptera . . . . . Roy A. Crowson
Cytogenetics of Insects . . . . . S. G. Smith
Population Genetics . . . . . Hannes Laven
Population Dynamics . . . . . H. G. Andrewartha and L. C. Birch
Host Selection of Phytophagous Insects . . . . . A. J. Thorsteinson
Evolution and Biology of Termites . . . . . Frances M. Weesner
Defense Mechanisms Against Insecticides . . . . . A. W. A. Brown
Insecticides in Relation to Public Health . . . . . Wayland J. Hayes, Jr.
Fundamentals of Locust Control . . . . . D. L. Gunn
Application of Insecticides . . . . . R. J. Coursheе
The Biology of Fruit Flies . . . . . L. D. Christenson and R. H. Foote
Recent Advances in Apiculture . . . . . Frank E. Todd
Recent Advances in Forest Entomology . . . . . V. Butovitch
Biological Relationships Between Lice and Microbial Agents . . . . . F. Weyer
Neurosecretion in Insects . . . . . William G. Van der Kloot
Chromosome Variation in Adaptation of Insects of Varied Environments . . . . . A. Brito da Cunha
Sampling Insect Populations . . . . . R. F. Morris
Citrus Insects and Mites . . . . . Lee R. Jeppson and G. E. Carman

Libraries, companies, other organizations and non-members should place their orders with: Annual Reviews Inc., Grant Avenue, Palo Alto, California. $7.00 per copy postpaid in the U.S.A., $7.50 per copy elsewhere.

ENTOMOLOGICAL SOCIETY OF AMERICA
1530 P Street, N.W.
Washington 5, D.C.

A Cyanamid Report:

What's new with Malathion?

New intervals for Malathion – Malathion continues to be the ideal material for late season insect control. Reduced intervals between last application and harvest were received on these crops in 1958:

Tomatoes – from 3 days to 1 day with malathion 57% Emulsifiable Liquid, malathion 25% Wettable Powder and malathion 4% to 5% dusts.

Pears – from 3 days to 1 day with malathion 57% Emulsifiable Liquid.

Cucumbers, Squash, Melons – from 3 days to 1 day with malathion 57% Emulsifiable Liquid, malathion 25% Wettable Powder and 4% to 5% dusts.

Brambleberry Family – from 7 days to 1 day with malathion 57% Emulsifiable Liquid, malathion 25% Wettable Powder and 4% to 5% dusts.

Extended interval: – The label for leaf lettuce has been extended from 10 days to 14 days. The label for head lettuce remains the same: 7 days.

New crop uses for Malathion – Label acceptance of malathion for insect control on figs and okra extends its already long crop use list to 95.

Okra – For the control of aphids. Use recommended rates of malathion Emulsifiable Liquid, Wettable Powder or dusts up to time pods start to form.

Figs – For control of dried fruit beetles and vinegar flies. Use Emulsifiable Liquid or dusts at recommended rates. Apply when necessary up to 3 days from harvest.

New animal claims – In addition to label acceptance for *direct application* on cattle, hogs, poultry, cats and dogs, malathion has received these labels for direct application on sheep, goats and swine:

For the control of lice, ticks and keds on sheep and goats. Apply 16 lbs. of malathion 25% Wettable Powder per 100 gallons of water. Spray animals thoroughly. Repeat application after 2 or 3 weeks if needed. Do not apply to milk goats. Do not treat animals under one month of age. When applying sprays, avoid contamination of feed, food containers and watering troughs.

For the control of lice on swine, use malathion 4% or 5% dust making a thorough application to the animals. In addition, pens should also be thoroughly dusted. Repeat application in 10 days, and thereafter as needed. Avoid contamination of feed, food containers and watering troughs.

Developer and producers of malathion and parathion.

American Cyanamid Company,
Agricultural Division, Dept. HE,
New York 20, N. Y.

CYANAMID
MALATHION
INSECTICIDES

the 3 best ways to stop insect damage!

HEPTACHLOR America's leading soil insecticide. Protects forage crops without contaminating milk or meat. Used to control a wide variety of insects on all major crops.

CHLORDANE America's leading lawn and garden insecticide. Used extensively by pest control operators for termite control, because of its long residual effectiveness.

ENDRIN A powerful new weapon in the war against crop damaging insects. Crop pests which previously were extremely difficult to control can now be killed easily and economically with Endrin.

VELSICOL

VELSICOL CHEMICAL CORPORATION

330 East Grand Avenue, Chicago 11, Illinois

Write for complete information!

International Representative Velsicol International Corporation, C. A., P. O. Box 1687—Nassau, Bahamas, B. W. I.

INDEX XVI

INDEX TO THE LITERATURE OF AMERICAN ECONOMIC ENTOMOLOGY

Number XVI of this series, which appeared in October, 1959, covers the literature for 1956 and 1957. The book contains 704 pages. Indexes I through XV covering the literature from 1905 through 1955 are also available.

Index XVI is bound in black buckram as are previous volumes. Helene G. Cushman, the Compiler of Index XVI, has carried on the high tradition of excellence set by her predecessors.

Price postpaid $6.00; to E.S.A. members $4.00

Order from

Entomological Society of America
1530 P Street, N.W.
Washington 5, D.C.

THOMAS SAY FOUNDATION

VOLUME I Sarcophaga and Allies of North America. By J. M. Aldrich. $4.50

VOLUME II The Plecoptera or Stoneflies of America North of Mexico. By J. G. Needham and P. W. Claassen. $5.00

VOLUME III Plecoptera Nymphs of North America. By P. W. Claassen. $4.00

VOLUME IV The Blow Flies of North America. By D. G. Hall. $6.50

VOLUME V Aphids of the Rocky Mountain Region. By Miriam A. Palmer. $10.25

VOLUME VI A Synoptic Catalog of the Mosquitoes of the World. By Alan Stone, Kenneth L. Knight and Helle Starcke. This up-to-date Catalog was published in October 1959. $7.25

All volumes are cloth bound and all are well illustrated. Volume IV has five colored plates, and volume V has eight.

Outside North America and U. S. Possessions, add 50¢ per volume to cover postage and handling. Registration or insurance at purchaser's expense.

Entomological Society of America

1530 P Street, N. W. **Washington 5, D. C.**

TABLE OF CONTENTS

PAGE

CLARK, ARNOLD M.—Oxygen Poisoning in Insects 637

MULLA, MIR S., AND RALPH B. MARCH—Flight Range, Dispersal Patterns and Population Density of the Eye Gnat, *Hippelates collusor* 641

SMITH, CLYDE F.—A New Species of Aphid on Sugar Maple (Aphidae: Homoptera) 647

KEIFER, H. H.—New Eriophyid Mites 649

BISHOP, GUY W.—The Comparative Bionomics of American *Cryptolestes* (Coleoptera-Cucujidae) That Infest Stored Grain 657

CHADWICK, L. E.—The Furcopleural Muscles of Lepidoptera 665

HEDEEN, ROBERT A.—Taxonomical Studies on the Larvae of the Genus *Psorophora* in the United States with Particular Reference to the Common Species of the Subgenus *Grabhamia* (Diptera: Culicidae) 668

SMITH, D. S.—Utilization of Food Plants by the Migratory Grasshopper, *Melanoplus bilituratus* (Walker) (Orthoptera: Acrididae) with Some Observations on the Nutritional Value of the Plants 674

TARSHIS, I. BARRY—Feeding *Culex tarsalis* on Outdated Whole Human Blood Through Animal-Derived Membranes (Diptera: Culicidae) 681

FLOYD, E. H., AND L. D. NEWSOM—Biological Study of the Rice Weevil Complex 687

PIPA, RUDOLPH L., AND EDWIN F. COOK—Studies on the Hexapod Nervous System. I. The Peripheral Distribution of the Thoracic Nerves of the Adult Cockroach, *Periplaneta americana* 695

CHIANG, H. C., AND A. C. HODSON—Population Fluctuations of the European Corn Borer, *Pyrausta nubilalis*, at Waseca, Minnesota,, 1948 to 1957 710

MIDDLEKAUFF, WOODROW W.—Some Biological Observations on *Sarcophaga falciformis*, a Parasite of Grasshoppers (Diptera-Sarcophagidae) 724

FRINGS, HUBERT, AND MABLE FRINGS—Reactions of Swarms of *Pentaneura aspera* (Diptera: Tendipedidae) to Sound 728

STEINHAUER, A. L., AND W. P. STEPHEN—Changes in Blood Proteins During the Development of the American Cockroach, *Periplaneta americana* 733

OATMAN, EARL R.—Host Range Studies of the Melon Leaf Miner, *Liriomyza pictella* (Thomson) (Diptera: Agromyzidae) 739

LAWSON, FRANCIS R.—The Natural Enemies of the Hornworms on Tobacco (Lepidoptera: Sphingidae) 741

KANNOWSKI, Paul B.—The Flight Activities of *Dolichoderus* (*Hypoclinea*) *taschenbergi* (Hymenoptera: Formicidae) 755

KOEHLER, C. S., AND GEORGE G. GYRISCO—Studies of the Vertical Distribution of the Clover Root Borer in Roots of Red Clover in Relation to Progression of the Season 760

SINHA, R. N.—The Hydrogen-ion Concentration in the Alimentary Canal of Beetles Infesting Stored Grain and Grain Products 763

SCIENTIFIC NOTES:

EWART, W. H., AND O. L. BRAWNER—*Haplothrips clarisetis* in Southern California (Thysanoptera: Phlaeothripidae) 765

BLOCK, BARTLEY C.—Strength-Weight Relationships in a Laboratory Population of *Tenebrio molitor* Adults 766

LEWALLEN, LAWRENCE L., AND LOREN M. NICHOLSON—Malathion Metabolism in Larvae of Resistant Mosquito Strains 767

BOOK REVIEWS 646

TRAVEL GRANTS 738

CHANGE OF ADDRESS 768

INDEX TO VOLUME 52 769